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Review of the Rate of Growth and Mortality of Pacific Salmon in Salt Water, and Noncatch Mortality Caused by Fishing

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Contents

1485 ABSTRACT

1485 RÉSUMÉ

1485 INTRODUCTION
- 1. Purpose
- 2. Notation
- 3. Error of estimates

1486 A. MORTALITY CAUSED BY FISHING BUT NOT INCLUDED IN CATCH STATISTICS

1486 Kinds of Mortality
- 4. Classification

1487 Losses from Gillnetting
- 5. Japanese studies of oceanic losses
- 6. American studies of oceanic losses
- 7. Losses from coastal gillnetting
- 8. Mortality among fish lost

1488 Losses from Longlining
- 9. Comparison

1488 Losses from Trolling
- 10. General considerations
- 11. Number of salmon released from trolls
- 12. Mortality among salmon released from trolls
- 13. Escapees and fish killed by predators

1490 Summary
- 14. Estimates of noncatch fishing mortality

1491 B. ESTIMATES OF OCEAN NATURAL MORTALITY RATES

1491 General Considerations
- 15. Sources of information

1491 Adjustment for the Marking Handicap
- 16. The problem
- 17. Pink salmon
- 18. Sockeye salmon
- 19. Chinook salmon

1493 Ocean Tagging Method
- 20. Procedure
- 21. Chinook salmon of southeastern Alaska

1494 Double Ocean Tagging Method
- 22. Procedure
- 23. Puget Sound cohos

1495 Smolt Survival Method
- 24. Procedure
- 25. Karluk sockeye (Ricker's estimates)
- 26. Karluk sockeye (Model 1 of Fredin)
- 27. Cultus Lake cohos

1496 Maturity Schedule Method of Parker
- 28. Procedure
- 29. Karluk sockeye
- 30. Cultus Lake sockeye
- 31. Lake Dalnee sockeye

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32. Hook Nose Creek sockeye
33. Hook Nose Creek pink and chum salmon

1498 Mortality Distribution Method
34. Procedure
35. Karluk sockeye (Model 2)
36. Karluk sockeye (Model 3)
37. Karluk sockeye (Model 4)

1499 Comparison of Life Histories Method
38. Procedure
39. Hook Nose chum salmon
40. Babine sockeye

1501 Maturity Schedule Method of Fredin
41. Procedure
42. Bristol Bay sockeye

1501 Ocean Immatures Method
43. Procedure
44. Bristol Bay sockeye

1502 Smolt Indices Method
45. Procedure
46. Karluk sockeye

1503 Dichotomy and Maturity Schedule Method
47. Procedure
48. Bristol Bay sockeye

1505 Limit-Mean Method
49. Procedure
50. Columbia River cohos

1505 Taguchi's Method
51. Procedure
52. Chum salmon
53. Sockeye salmon

1506 Cleaver's Method
54. Procedure
55. Columbia River fall chinooks

1507 Inverse Weight Method
56. Procedure
57. Puget Sound cohos
58. Karluk sockeye

1509 Comparison of Mortalities Method
59. Procedure
60. Karluk sockeye

1510 Summary of Natural Mortalities
61. Sockeye
62. Pinks, chums, cohos, and chinooks

1513 C. Estimates of Rate of Growth

1513 General Considerations
63. Age determination
64. Selective sampling
65. Weight–length relationships

1513 Tagged Salmon Method
66. Procedure
67. Sockeye, pinks, and chums
68. Sockeye south of the Aleutian Islands

1514 Ocean Sampling Method
69. Procedure
70. Bristol Bay sockeye
71. Pink salmon
72. Chum salmon
73. Coho salmon

1515 Back-Calculation Method
74. Procedure
75. Sockeye salmon
76. Pink Salmon
77. Chum salmon
78. Chinook salmon

1516 Method of Comparing Adult Sizes at Successive Ages
79. Procedure
80. Sockeye salmon
81. Chinook salmon

1517 Summary
82. Growth by species and region

1518 D. Comparisons of Yield With and Without Ocean Fishing

1518 Gain in Yield from Fish now Being Caught or Destroyed by Ocean Gear
83. Balancing positive and negative factors
84. Sockeye salmon
85. Pink salmon
86. Chum salmon

1520 Gain in Total Yield from Discontinuing Ocean Fishing on the Scale that now Exists
87. Procedure
88. Pink salmon
89. Sockeye salmon
90. Chinook salmon

1522 Acknowledgments

1522 References

Abstract

RICKER, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. J. Fish. Res. Board Can. 33: 1483–1524.

Mortality (other than landed catch) caused by pelagic gillnetting is estimated to be equal to the catch, for salmon in their penultimate year of life, and equal to about a quarter of the catch for salmon in their final year of life. Mortality caused by trolling for coho (*Oncorhynchus kisutch*) and chinook salmon (*O. tshawytscha*) averages about one fish killed (mostly below legal size) for every two that are boated. The natural mortality rate for sockeye salmon (*O. nerka*) in their final year of life averages about 0.015 per mo and is somewhat more in earlier years of pelagic life; the greater part of natural mortality after the smolt stage occurs during the downstream migration and early months of "coastal" life. For coho and chinook the best natural mortality estimate for the last year of life is 0.013 per mo, and that for pink (*O. gorbuscha*) and chum (*O. keta*) is of the same order. Growth rates during the final growing season vary from 0.26 per mo for pink and coho salmon to 0.06 per mo for chinook in their 5th ocean yr. Gains from ceasing to take immature salmon on the high seas range up to 300% of the catch now being taken in that category, while for fish taken in their final year they range up to about 70%, depending on the time of year at which the fishing is done. Gains from transferring existing pelagic net fisheries to the coastal region would be 76% (North American sockeye) and 86% (Asian sockeye) of the weight of fish now caught pelagically. Gains in total yield of existing salmon fisheries (pelagic and coastal) are estimated as 78% for Asian pink salmon and 72% for Asian sockeye. The increase in weight of the total catch from discontinuing ocean trolling for Columbia River chinook salmon and increasing river fishing correspondingly is estimated tentatively as between 63 and 98%.

Résumé

RICKER, W. E. 1976. Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing. J. Fish. Res. Board Can. 33: 1483–1524.

On estime que la mortalité (autre que la prise débarquée) causée par la pêche pélagique au filet maillant est égale à la prise pour des saumons dans l'avant-dernière année de vie et à environ un quart de la prise dans le cas de saumons dans leur dernière année de vie. Pour les saumons coho (*Oncorhynchus kisutch*) et chinook (*O. tshawytscha*), la mortalité causée par la pêche à la traîne est en moyenne d'environ un poisson tué (au-dessous de la taille légale pour la plupart) par deux saumons capturés. Le taux de mortalité naturelle de saumons nerka (*O. nerka*) dans la dernière année de vie est en moyenne d'environ 0.015 par mois et est quelque peu plus élevée durant les années de vie pélagique précédentes; la plus grande partie de la mortalité naturelle après le stade de smolt se produit au cours de la migration en aval et durant les premiers mois de vie «côtière». Pour les saumons coho et chinook, la meilleure estimation de mortalité naturelle durant la dernière année de vie est de 0.013 par mois, et celle des saumons roses (*O. gorbuscha*) et keta (*O. keta*) est du même ordre de grandeur. Le rythme de croissance durant la saison de croissance finale varie de 0.26 par mois pour le saumon rose et le saumon coho à 0.06 par mois pour des saumons chinook dans leur 5^{e} a. de vie en mer. Si l'on cessait de capturer des saumons immatures en haute mer, les gains iraient jusqu'à 300% des prises actuelles de cette catégorie, alors que pour les poissons capturés dans leur dernière année, les gains iraient jusqu'à environ 70%, selon le temps de l'année où la pêche est pratiquée. Les gains résultant d'un transfert de la pêcherie pélagique au filet maillant vers la région côtière seraient de 76% (saumon nerka nord-américain) et de 86% (saumon nerka asiatique) du poids des poissons présentement capturés en haute mer. On estime à 78% pour le saumon rose asiatique et à 72% pour le saumon nerka asiatique les gains dans le rendement total des pêcheries de saumon existantes (pélagique et côtière). L'augmentation de poids des prises totales qui résulterait d'un arrêt de la pêche à la traîne en mer du saumon chinook du fleuve Columbia et d'une augmentation correspondante de la pêche dans le fleuve est estimée provisoirement à 63–98%.

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Introduction

1. PURPOSE

During the 1970s the problem of conservation of Pacific salmon has become increasingly acute. An important aspect of the problem is the effect of offshore fishing on the total salmon harvest. This document reviews the information on the subject that has come to the author's attention up to early 1975. The species of salmon considered are the chinook (*Oncorhynchus tshawytscha*), chum (*O. keta*), coho (*O. kisutch*), pink (*O. gorbuscha*), and sockeye (*O. nerka*).

2. Notation

Life histories of salmon are designated in terms of growing seasons in fresh water and in the ocean. For example, at maturity a pink salmon is 0/2 (0-freshwater, 2-ocean), showing little or no freshwater growth and the whole or part of 2 growing seasons in the ocean. A typical mature Cultus Lake sockeye is 1/3 (1-freshwater, 3-ocean), showing 1 growing season in the lake and part or all of 3 in the ocean. The last ocean season is not a complete growing season because the fish returns to fresh water during the summer or fall of its final year of life. Also, there can be some freshwater growth at the start of the second growing season among sockeye and cohos, but this is ignored and all that year's growth is referred to as the 1st yr of ocean growth. Similarly a chinook salmon that goes to sea in its 1st yr is called 0-freshwater, even though it may have made a good deal of its first season's growth in fresh water.

Other systems are used in other papers, and it is necessary to be careful in interpreting them. For example, Fredin's (1964, 1965) designation of the mature 1-freshwater 3-ocean sockeye above would be "2-freshwater, 2-ocean," with the symbol 4_2 or 4·2, while Mathews (1968) would call it "1-freshwater, 2-ocean" with the symbol 1·2 (= 1/2 of Parker 1963). For immature fish the terminology varies because different authors use different definitions of the time at which a year of ocean life starts and ends. Here we use the symbol + for immatures; for example a 1-freshwater sockeye in its 3rd ocean growing season is 1/2+, and is called a 2+ ocean fish.

3. Error of Estimates

In assessing the reliability of different estimates of mortality rates, etc., four kinds of error can be distinguished. The *first* is random error resulting from the small numbers of fish counted in certain experiments, when these are a sample of a considerably larger body, either actually or potentially. Such numbers tend to have a variance approximately equal to themselves. For example, suppose a sample of 1,000 fish from a catch of 100,000 contains 50 marked individuals. The sampling variance of the 50 is 50, and its 95% confidence limits are approximately $50 \pm 2\sqrt{50} =$ 36–64.

The *second* type of error is variability associated with environmental differences from year to year. For example, the marine survival rate of smolts might be 10% one year, 15% the next, and 8% the year following. The mean and confidence limits of a series of this sort can be estimated using standard statistical procedures. If random error exists in the experiment, it will be confounded with effects of environmental variability and included in the confidence limits estimated from replication, which is all to the good. If only a single estimate is available, some idea of its reliability may be obtainable from comparisons with similar estimates made at other places, but no reliance should be placed on purely statistical variability except as a *minimum* estimate of the actual dispersion.

A *third* type of error stems from the existence of potential variables affecting the result, whose magnitude and sign are unknown. For example, in the comparison of life histories method of Section 38 there is an assumption that the pink and chum salmon from a particular stream are equally vulnerable to the fishing in progress. The two species are taken using purse seines, so that mesh selection is unlikely, but there is no guarantee that this makes them equally vulnerable, particularly since chums migrate somewhat later in the season. Thus there is potential bias in the assumption of equal vulnerability, but no information concerning its direction or magnitude.

The *fourth* type of error is that which is usually called systematic error. Some aspect of an estimate biases it in one direction or the other, and the direction of this bias is known, but its magnitude can be estimated only crudely or not at all. Such estimates are not necessarily useless. They can be used as a maximum (or minimum) estimate of the parameter in question, which is often of real value. However a biased estimate will usually also be subject to errors of types 1 and 2, and care must be taken that these are not so great as to make it likely that the estimate could in fact err in the direction opposite to that indicated by its systematic bias.

Finally, we might note at any life-history stage where natural mortality is small the natural survival rate will not differ greatly from 100%. A series of estimates of survival rate may frequently include values greater than 100% because of sampling error. Although such values are impossible taken by themselves, they should not be rejected when computing averages, otherwise the result will be biased (survival estimate too small, mortality too great).

A. Mortality Caused by Fishing but not Included in Catch Statistics

Kinds of Mortality

4. Classification — The principal types of losses caused by salmon fishing gear, other than

the reported catch, may be classified as follows: 1) Salmon that are attacked by a predator while in the gear and are removed or are so badly damaged that they are not landed. 2) Salmon that have been caught, but subsequently free themselves and die later from wounds or overexertion, or from predation or disease resulting from their impaired condition. Such deaths may occur up to many days or weeks later; for example, Petrova (1964) found that net-marked sockeye died in fresh water, without spawning, more often than did unmarked ones. In troll fishing a fish may escape after very strenuous exertions, which sometimes lead to death. 3) Salmon that have been caught and killed in the gear but drop off before the gear is hauled in. Categories 2 and 3 are called "dropouts" by French and Dunn (1973). We may distinguish "passive dropouts" (3) from "active dropouts" or escapees (2). 4) Salmon that have been caught and killed and drop off the gear after they come into view as the gear is being hauled into the boat. Usually this happens when they lose the buoyant support of the water. These are the "fallouts" of French and Dunn. In sportfishing and in many commercial operations most, but not all, of the potential loss of this sort is avoided by using a dipnet or gaff. 5) Salmon less than legal size, or caught during a closed period for the species in question, that are discarded dead or mortally injured — either after being boated, or by shaking them off or out of the gear as it is hauled up. Again the fish may die only after a considerable lapse of time. In troll fisheries sublethal or out-of-season salmon are called "shakers" — whether they are simply jerked off the hook or are removed with great care. 6) Salmon caught but not reported. These may be the incidental catch of another fishery, fish consumed at sea or taken for home use by fishermen, or the catch of an illegal commercial operation. The catch of sport fishermen is usually not reported directly, but their take is estimated by some kind of sampling or survey system, hence it is not included in this category.

Of the six categories above, 1, 2, 3, and 4 are suspected of having considerable importance in gillnet and longline fisheries, while 1, 2 and 4, and especially 5, may be important in trolling. Salmon caught in nets or on lines that are "soaked" for long periods are most susceptible to predation and escape, while rough water tends to increase passive dropouts and fallouts. Seines cause little or no damage of types 1–4, but can take substantial numbers of sublegal chinook salmon, which have been observed to suffer large mortality before release (S. B. Mathews personal communication). Trapnets and fishwheels are not known to cause appreciable losses of types 1 through 5. All gears may be involved in category 6, but this is not usually considered an important source of loss. All six categories of loss have one thing in common, that while they can readily be demonstrated to occur, it is difficult to obtain quanititative information concerning them.

Losses from Gillnetting

5. Japanese studies of oceanic losses — Doi (1962b) reported Sasaki's observations of the catch in a gillnet at ½-h intervals and found that rates of dropout plus predation were up to 55% for coho and 47% for sockeye after 5 h. The rate of loss tended to increase with time. In a companion paper (1962a) Doi used trial values of instantaneous rate of loss from 0 to 0.5, and stated that the latter figure, which corresponds to 39% actual loss, is supposed to apply to offshore fisheries for pink salmon.

Konda (1966) cites studies by C. Miyazaki and H. Taketomi, who estimated a 20% loss of pink salmon from gillnets. Konda himself concluded that "high seas salmon fishing is always accompanied with a large loss of resources."

Ishida et al. (1969) used underwater television to observe losses from gillnets, and found 4–25% loss in 4 trials (mean 16%). Losses were greater from the smaller of the two mesh sizes used. Since the experiments were conducted off the coast of Kamchatka, it is likely that large (maturing) fish were mainly involved.

6. American studies of oceanic losses — French and Dunn (1973) have the most extensive data on noncatch losses avilable up to now. Comparison of sockeye catches in ocean gillnets set for 6–9 h were made with those set every 3 h. These showed losses of 20–32% in 9 h in preliminary experiments of 1964, and a 27% average for 3 h in more extended trials in 1965. They observed qualitatively that predators were responsible for part of this loss. By watching the net from small boats in 1966, dropout plus predation rates were observed of 42–48% from large-meshed nets and 40–46% for smaller meshes, for periods up to 11 h. More intensive patrolling of the nets in 1967 gave somewhat higher values: 11% for 1 h, 17% for up to 2.5 h, 58% for up to 5 h, and 64% for up to 10 h. In this case large-mesh nets had fewer losses than small: 58% vs. 83% for up to 10 h. It was also found that multifilament nets had a greater loss rate (86%) than monofilament (41%).

Whereas French and Dunn's 1967 results concerned immature sockeye, in 1968 smaller rates of loss were observed for maturing fish, 20% for

up to 10 h, and there was little difference between monofilament and multifilament. They noted also that the weather in 1968 was unusually calm, whereas in 1967 it had been unusually stormy.

Observations in 1969 were limited because of stormy weather, but loss rates were generally smaller than in 1967 and 1968. Even so, losses of 15% for up to 10 h were observed with maturing fish and 35% with immature fish; again there was no consistent difference between multifilament and monofilament nets.

French and Dunn also related dropout-plus-predation rates to wind speed and obtained positive though statistically nonsignificant results, particularly at the greater distances from land where predators were less in evidence.

As regards "fallouts," French and Dunn (1973) found these to be about 1.4% of the fish boated during high-seas gillnetting, practically all of which were dead.

7. Losses from coastal gillnetting — Gillnets fished in bays and estuaries close to the coast or in the lower reaches of rivers are usually set for short periods of time, typically 1–3 h. The sea surface is much calmer than on the high seas, and boats are smaller; also the nets are shorter and they may be frequently patrolled. For all these reasons dropouts and fallouts are rare; also, large predacious fishes are absent, and mammalian predators tend to be scared off by the attending boat, sometimes by gunfire. French and Dunn (1973) made 8 sets in Puget Sound of up to 3 h duration, and observed no losses from among 59 fish spotted. They also quote a Puget Sound study by Jewel (1970) that showed 1.2% dropouts among 245 salmon spotted in commercial nets. However, when sockeye of a small-sized race were taken in nets too large for them, there was 29% loss (including escapees). On the other hand, in the Fraser gillnet fishery escapees can be fairly numerous, although the high percentage of net-marked sockeye observed by Thompson (1945) below an obstruction is not necessarily typical of the run as a whole, because fish weakened by their struggle in a net would be less capable of passing a difficult spot on their migration route.

8. Mortality among fish lost — How many of the salmon lost from ocean gillnets survive? Obviously those taken by predators and the passive dropouts do not, so this concerns only the salmon that actively escape the net (our category 2). French and Dunn (1973) summarize the extensive evidence that salmon caught in high-seas gillnets and tagged are rarely recaptured, the immature ones almost never, whereas those taken on longlines and tagged are recovered with much greater frequency, though by no means as frequently as would be expected of uninjured and untagged fish. Direct experiments with salmon that escaped from a gillnet in salt water showed that 73% died in captivity as compared with 10% for controls (Thompson et al. 1971; Hunter et al. 1972). In nature the loss would presumably be greater if there were predators in the region.

For salmon taken in their home river the situation is different. There they have begun to acquire the physiological resistance to injuries and the thicker and tougher skin that characterizes their last few months of life. For example, Parker (1960) found that chinook salmon taken by gillnet and tagged in the lower Taku River suffered no mortality, whereas troll-caught fish of similar size taken in the ocean, had substantial mortality.

Losses from Longlining

9. Comparison — Japanese longlining for salmon on the high seas, much of it in the same area as ocean gillnetting, was carried out by a landbased fishery before it was discontinued in 1972. Losses during longlining have apparently not been studied, but the same opportunities for predation, escape, dropoff, and falloff exist, so provisionally the same mean losses may be estimated.

Losses from Trolling

10. General considerations — The troll fishery is apparently restricted to the eastern side of the Pacific. It operates up to about 25 miles from the coast, much of it in exposed waters, although there are important sport fisheries and commercial operations in Puget Sound, the Strait of Georgia, and the various protected channels northward.

Undersized salmon hooked during trolling are called "shakers" because they are often just shaken off the hook, and most concern and experimentation has been with these sublegal individuals. Legal size limits have varied with time and region. A general tendency to increase minimum sizes has automatically increased the importance of the shaker problem, while at the same time reducing the loss from landing fish that have a very large growth potential (Anon. 1970).

11. Number of salmon released from trolls — Pitre (1970) reported on voluntary logbook reports from commercial trolling operations off British Columbia in 1968 and 1969. There the chinooks less than 60-cm fork length are sublegal, as are all cohos caught before June 16. During mid-April–

TABLE 1. Results of logbook and research observations on sublegal catches in the British Columbia troll fishery of April 15–June 15. The total legal chinook salmon (*Oncorhynchus tshawytscha*) catch is shown under "Logbook," and the catch per troll day under "Research," (Pitre [1970], tables 1, 4, and 5).

	Logbook		Research								
			Plugs		Spoons		Hoochie		Combined		
	1968	1969	1968	1969	1968	1969	1968	1969	1968	1969	Both
Legal chinooks	143,800	146,300	5.4	5.2	8.1	7.6	4.7	6.0	5.7	6.3	6.0
Ratios											
Chinook shakers to legal chinooks	0.44	0.52	0.52	0.37	1.10	1.58	1.89	1.02	1.20	1.06	1.13
Cohos to legal chinooks	1.65	0.71	3.15	0.73	5.20	1.95	13.38	3.50	7.09	2.11	4.49

mid-June the sublegal chinooks reported were 44 and 52% of those landed (Table 1). Coho shakers were reported as 165% and 71% of the *chinooks* landed (no cohos could be landed at that time). After June 15 3rd-yr cohos are mostly above legal size.

In addition, direct observations on chartered vessels were made in 1968 and 1969 from mid-April to early June on the chinook fishing banks, the operators being instructed to fish normally without either seeking or avoiding areas where shakers were numerous. Table 1 summarizes Pitre's tables 1, 4, and 5. Three different types of lure were used, all in commercial use: plugs, spoons, and a hook covered by a rubber "hoochie" skirt, with a flasher farther up the line. Plugs caught considerably fewer sublegal chinooks and cohos than did the other two lures; unfortunately they also caught somewhat fewer legal chinooks, so were not in the highest favor with regular fishermen. Ratios of the combined catches for all the lures and both years are 4.5 cohos and 1.1 sublegal chinooks for each legal chinook caught. These figures are much greater than appeared in the logbook records. One possible reason would be a natural desire to minimize losses, on the part of the commercial operators.

Table 1 shows that cohos were much more numerous in 1968 than in 1969. In both years, the coho shakers reported in the logbooks amounted to 13% of the legal troll catch of cohos taken later in the season. Comparison with the research results increases this to 56% in 1968 and 39% in 1969.

Washington information (Anon. 1969) for the years 1948–55 was also obtained by voluntary reporting. Sublegal to legal ratios reported for chinook salmon varied from 0.07 to 0.21 between March 20 and June 14, with a mean of 0.13. However, observations by fishery employees in 1968 gave a ratio of 1.4 in late May and early June and as much as 15.7 in late June and July. Observations were also made on the sport fishery off the outer coast, where the legal limit for chinooks is 20 in. total length (46.5-cm fork length). It was concluded that "in recent years ... the chinook shaker catch prior to June 15 at least equals and probably slightly exceeds the catch of legal-sized fish."

O'Brien et al. (1970) reported that in California sublegal chinooks and cohos released equalled 71% of the fish landed in 1968 and 65% in 1969, as indicated by voluntary logbook records from commercial fishermen. These represent 630,000 and 485,000 fish, respectively, when applied to the total catch, about half chinook and half coho.

Oregon studies reported by Reed (1970) and also by O'Brien et al. (1970) were based on observation by trained personnel throughout the fishing season and revealed sublegal to legal ratios of 0.4–3.4, with an average of 1.69 (excluding one value of 7.5 based on very few fish). However, O'Brien et al. note that the experimental fishing was concentrated in areas where small fish were known to be more numerous than average. As in California, shakers were most numerous in spring and fall, when sublegal cohos and chinooks respectively were numerous, but they were also quite common in summer.

Summarizing the California and Oregon data together with those for Washington and British Columbia, O'Brien et al. concluded that "the Pacific Coast chinook shaker catch approximates (in numbers) the legal chinook catches."

12. Mortality among salmon released from trolls — How many of these shakers die? Working in the Strait of Georgia, Milne and Ball (1956) observed 34% immediate mortality from catching coho salmon of 38–61-cm fork length, and an additional 7% died in a holding pond later. They note that their catching procedure was less severe than what occurs in commercial trolling; however, the fish were tagged with a Petersen tag below the dorsal fin after being caught. Considering only fish that seemed to be in good condition, mortality was 33%. Fish hooked in the

gills all died, of those hooked in the eye about half died, while 22% of those hooked in the jaw died. A few coho "grilse" of 20–41 cm, which are commonly hooked in the sport fishery in late summer and fall, showed an even larger rate of loss (77%).

Parker (1960) estimated a direct loss of 20% from experiments with chinooks in Alaska, and a delayed mortality of 40–86% was found in experiments by Parker and Black (1959) and Parker et al. (1959).

Van Hyning (1968), as reported by Wright (1970), concluded that 40% mortality was a "not unreasonable" estimate of loss among chinooks, based on holding studies.

Lasater and Haw (1961) and Haw (1963) report on recoveries of cohos of fork length 28–50 cm (avg 40.3 cm), and chinooks of 19–60 cm (avg 36.6 cm), that were caught on sport trolling gear in April and May in Puget Sound, tagged with a "spaghetti" tag, and released. Overall rate of recovery was 22.2% for cohos and 17.6% for chinooks, including freshwater recoveries. No recaptures were obtained from fish hooked in the gills, but relatively few suffered such injury. Smaller fish were retaken less frequently than larger ones, but a greater tag loss from small fish may partly account for this.

Lasater and Haw discuss their results as follows: "After a salmon is tagged and released it is subject to disease and predation, tag loss occurs, some tags are not turned in by fishermen and there is an unseen spawning escapement. In spite of this 22.2% of the tags put out were returned. This seems an unlikely happening if hooking mortality were high." However, their data can easily accommodate a hooking mortality of up to 40% or so, and still leave room for the other types of loss. The rate of return of coho tags was only 19% from fisheries whose overall rate of exploitation was 70–80% (Section 57). Anticipating the results of Section B, the natural mortality rate of these fish should not exceed 0.02 per mo or 0.08 for 4 mo; in competition with other kinds of loss this would account for about 4% of the tags. This leaves 36% for tag loss, nonreporting, and escapement if hooking mortality were 40%.

P. T. Jensen, as reported by Wright (1970), observed an immediate hooking loss of 32% for cohos in California, and a total loss "greater than 60%."

Wright (1970) reviewed published and unpublished information, and listed 35 experiments in a summary table, including those mentioned above. Mortality estimates varied from 1.9% for cohos (immediate mortality only) to 71% for chinooks held for an extended period in a tank. Wright concluded that an average figure less than 10% is "virtually impossible" in the fishery for either species; also that "rates below 15% or above 45% are quite difficult, if not impossible." Within this range he favored a figure not greater than 30%, but this apparently excludes "seriously injured fish."

In addition to cohos and chinooks, there was one experiment with pink salmon. It indicated 13% mortality among fish that were nearing fresh water.

Wright (1970) also observes that rapid hauling in of lines, roughly shaking fish off the hook or clubbing them to make their removal easier, must all increase mortality above the values quoted. Since at least the first two of these are common practices, an overall estimate of 50% mortality seems rather conservative.

The combination of 50% mortality with a shaker incidence equal to the catch means that 1 chinook is killed for every 2 that are boated. If the 30% mortality rate is used, mortality becomes 1 killed for every 3.3 boated. The data quoted for cohos above suggest similar rates of loss.

13. Escapees and fish killed by predators — The above studies do not shed light directly on losses among fish that escape from troll gear by their own efforts. Since these tend to be the larger fish, and presumably those that are not too firmly hooked, the damage they suffer is probably much less than that of the shakers. Also, even fairly severe damage to the jaw is not necessarily fatal, as shown by deformed maxillary bones, etc., on healthy fish caught subsequently. At a guess, losses from this cause are probably less than 10%.

Removal of salmon from troll lines by predation is assumed to have occurred when a fish is lost from the hook and a seal or sea lion is observed in the vicinity. In addition, Dr S. B. Mathews tells me that blue sharks (*Prionace glauca*) cause considerable losses in late summer off the Washington coast, "commonly several per boat-day at this time of year, and perhaps 20–30 on a bad day." Similarly dogfish (*Squalus suckleyi*) can be a nuisance in Puget Sound and the Strait of Georgia.

Summary

14. Estimates of noncatch fishing mortality — All who have studied the question agree that important losses occur in high-seas fishing with gillnets. Experimental results show that the loss of

immature fish can scarcely be less than 50%, i.e. 1 fish killed for every 1 landed. For fish in their final year it averages about 25%, or 1 fish dead for every 3 landed.

Coastal and river gillnetting cause much less mortality than ocean gillnetting. Calmer weather, shorter sets, fewer predators, etc. are partly responsible, and partly it is because the fish have become much hardier physically and physiologically as maturity approaches, so that gillnet capture and escape is much less serious for them.

Longlining losses have not been studied but may resemble those from ocean gillnetting.

Mortality caused by trolling for coho and chinook salmon appears to be approximately 1 fish killed for every 2 that are boated.

B. Estimates of Ocean Natural Mortality Rates

General Considerations

15. Sources of information — Although estimation of natural mortality rate in the ocean is inherently a difficult problem, its importance has stimulated biologists to display remarkable ingenuity in devising methods that might work. Nearly all of these employ data that were collected primarily for another purpose. Particularly extensive use has been made of the sockeye salmon reproduction studies of J. T. Barnaby and R. E. Foerster in the late 1920s and 1930s, and of the high-seas fishing done by A. C. Hartt and his collaborators during the 1950s and 1960s.

Although it did not attempt to distinguish between deaths from fishing and those from natural causes, the first estimate of ocean mortality rate in the final year of life was by Murphy (1952), using the "dichotomy" method. Murphy's work was influential in leading Mathews (1968) to include a dichotomy estimate in his approach to the problem, while Parker (1962b) says that Murphy's paper served as a starting point in the development of his "maturity schedule" method.

Adjustment for the Marking Handicap

16. The problem — Several estimates of natural mortality rate are based on the survival of fry or smolts that have had one or both ventral fins removed, and sometimes the adipose as well. Absence of these fins imposes a handicap throughout the life of the fish, presumably in crisis situations. This has been demonstrated by direct experiment with pink salmon fry by Parker et al. (1963, table 2). They marked one lot by removing the adipose and right ventral fin and gave another lot a dummy handling routine. Marked and unmarked fry were held together in an aquarium along with a trout. Over a period of weeks the latter ate proportionately more marked than unmarked fry. In 4 experiments the mean "handicap ratio" (the ratio of the instantaneous mortality rates of marked and unmarked fry) was 1.35 (range 1.29–1.42). Another illustration of the existence of a continuing handicap from marking is the fact that adult sockeye that had been marked as smolts were much less successful in passing a serious obstruction in the Babine River than were unmarked ones (Ricker 1962a, appendix 6). Direct observations on the severity of the handicap in nature are available for pink, sockeye, and chinook salmon as described in the Sections to follow.

17. Pink salmon — Parker et al. (1963) summarized returns from 5 experiments where marked and unmarked pink salmon fry were released in nature, and Parker (1964) provided one more. Table 2 summarizes these experiments (see also table 1 of Parker et al. 1963). Only for Hook Nose 1961 is an estimate of rate of fishing available; it is a surprisingly large one, 3.07. Parker considers this to be larger than for other stocks in the region, and it must also be larger than in most years at Hook Nose Creek, otherwise the stock could not persist. For the other experiments handicap ratios are shown for 2 trial rates of fishing, 0.5 and 1.6, corresponding to a moderate rate of exploitation (39%) and a moderately large one (80%).

The McClinton Creek data are fairly consistent, and the following argument makes them even more so. It can reasonably be presumed that years having the poor overall survival rates would be years of a heavy fishery. On this basis the most likely handicap ratios for natural mortality alone would be those marked by an asterisk in the Table. The mean of the three that include a ventral fin mark is 1.492, which is practically the value (1.5) suggested as a likely mean by Parker et al.

The Hook Nose handicap ratios, by contrast, are rather inconsistent with each other. It seems best to put confidence in the later one, where rate of total return was known from observation.

In summary, the best available handicap ratio for pink salmon marked at the fry stage using one or both ventral fins is probably 1.49, from the McClinton experiments as adjusted above. The ratio 1.37, from the second Hook Nose experiment, is the only one based on an actual estimate of the total return. Anyone wishing to be conservative could use that figure, or perhaps the mean of the two, 1.43.

TABLE 2. Survival rates, instantaneous mortality rates, and handicap ratios for marked pink salmon (*Oncorhynchus gorbuscha*). Fins removed were: Ad = adipose, RV = right ventral, BV = both ventrals. (Parker et al. [1963] and Parker [1964].) Asterisk indicates most likely handicap ratio for natural mortality.

Experiment	Mark	Survival rate		Instantaneous mortality rate (including fishing)			Handicap ratio without fishing	
		Marked	Unmarked	Marked	Unmarked	Ratio	$F = 0.5$	$F = 1.6$
McClinton Creek								
1931	Ad	0.000517	0.002982	7.567	5.815	1.301	1.330	1.416*
1933	BV	0.027244	0.070816	3.602	2.648	1.360	1.444*	1.910
1935	AdRV	0.000399	0.004182	7.826	5.477	1.429	1.472	1.605*
1939	BV	0.004372	0.019076	5.432	3.959	1.372	1.428*	1.624
Hook Nose Creek								
1948	BV	0.009549	0.052154	4.651	2.954	1.575	1.692	2.253
1961	BV	0.005846	0.010089	5.142	4.596	1.119	1.369(for $F = 3.07$)	

18. Sockeye salmon — For sockeye there is information from two localities, Cultus and Babine Lakes. Rates of mortality of marked and unmarked smolts while at sea are compared in Table 3. Data are given for total mortality, and also for natural mortality only using the assumption that marked and unmarked adults are equally vulnerable to fishing. The Cultus Lake data are from experiments of R. E. Foerster summarized in tables D and E of Ricker (1962a). The primary observations are the total mortality rates from smolts marked in 1927 and 1928, which returned to the lake mainly in 1929 and 1930. The natural mortality rates are obtained by subtracting one of the two available estimates of fishing mortality rates, 1.41 for 1933 and 0.73 for 1932. In the odd-numbered years the large pink salmon runs prolonged and intensified salmon fishing at the time the Cultus sockeye were running, so the figure 1.41 is applied to the 1927 smolt experiment and 0.73 to the 1928 experiment (Table 3, Part B).

The Babine Lake data are for markings done in 1946, 1947, and 1948, the same mark (BV) having been used in all 3 yr. There are some approximations involved in the estimates of returns, but none are serious (Ricker 1962a, appendix 4). Survival of unmarked smolts was estimated somewhat later, for the smolt migrations of 1955–58; their natural mortality rate averaged 3.02 (range 2.46–3.67). Returns of both marked and unmarked fish included the catch as well as the escapement; consequently the primary information for Babine in Table 3 is the natural mortality rate shown in Part B. The rate of exploitation was estimated for the years 1949 and 1950 as 0.53 and 0.57, respectively, from the marked fish in the catch and the escapement (Ricker 1962a, table J). The mean value 0.55 is converted to an instantaneous rate of fishing of 0.80 and is added to the natural mortality rates to give the total figures in Part A of Table 3.

TABLE 3. Summary of estimates of instantaneous mortality rates of marked and unmarked young sockeye salmon (*Oncorhynchus nerka*), from marking to return. Total mortality rates include the fishery; natural mortality rates exclude it.

	Marked	Unmarked	Ratio
A. Total mortality			
Cultus 1927	4.74	3.69	1.28
Cultus 1928	4.31	3.43	1.26
Babine 1946–48	4.83	3.82	1.26
B. Natural mortality			
Cultus 1927	3.33	2.28	1.46
Cultus 1928	3.58	2.70	1.33
Babine 1946–48	4.03	3.02	1.33

In summary, the mean of the handicap ratios for sockeye in Part B of Table 3 is 1.37, suggesting that marked fish are 37% more vulnerable to natural sources of mortality throughout their life. This handicap ratio can be used to convert other estimates of natural mortality of marked sockeye to terms of unmarked fish.

Ricker (1962a), and following him Parker (1962b, 1963) and Fredin (1964, 1965), erroneously applied the mean handicap ratio 1.27 from the *total* mortality rates at Cultus Lake to adjust estimates of *natural* mortality rates elsewhere. Consequently all their instantaneous natural mortality estimates for sockeye are too great. In this paper they are divided by $1.37/1.27 = 1.079$ to obtain more representative values.

19. Chinook salmon — Cleaver (1969, table 15) compared the rate of return of marked and unmarked hatchery-reared chinook salmon to two Columbia River hatcheries. All the marks included the adipose fin (Ad) and the left or right maxillary bones (LM and RM). Some lots also had one or other of the ventral fins removed (LV and RV). These marks are more severe than

those used on the pinks and sockeye above.[1] Table 4 shows that marked fish returned to the hatchery much less frequently than the unmarked ones; and at each hatchery the fish with the additional LV mark returned less frequently than those without it, as would be expected. Cleaver points out that the lower percentage return of marked fingerlings can have several causes: 1) straying of marked fish to other streams; 2) a slightly greater total natural and fishing mortality rate because of their slightly longer life at sea; 3) somewhat greater natural mortality at a given age because of their slower growth; and 4) greater natural mortality related to the mark itself, presumably because of greater vulnerability to predation. He had a rough estimate of the straying effect, but item 4 above apparently had much the greatest importance. Table 4 shows that the overall handicap ratios are in the range 1.10–1.20. Assuming that fishing mortality (other than that mentioned under 2 above) is the same for marked and unmarked, it should be subtracted to get a handicap ratio for natural mortality alone. Cleaver's table 29 indicates that the instantaneous rate of ocean fishing for marked fish is of the order of 1.0, to which must be added a shaker loss of about 0.5 (Section 14). There is also a river fishery that has a rate of exploitation of about 67%, so that its instantaneous rate of fishing is $\log_e 0.33 = 1.12$ (from the AdRM returns in Cleaver's table 26). This figure includes the effect of straying, so the effect of the fishing alone would be slightly less, say 1.1. The total rate of fishing on these chinooks would therefore be about 2.6. In Table 4 this figure is subtracted from the total disappearance rates, and the handicap ratios increase to 1.16–1.34, with a mean of 1.23. This is still smaller than the mean value 1.37 obtained for sockeye. Several explanations are possible, of which the simplest is that chinooks may be a "tougher" species than sockeye and better able to compensate for a physical handicap. Another possibility is that the harmful effect of a mark decreases as the adult size of the fish increases; the order pink → sockeye → chinook corresponds with increasing size and decreasing handicap ratio.

[1]In his figure 3 Cleaver shows that marked chinooks grew more slowly than unmarked, the mean difference being 2.71, 1.97, and 0.99 cm at ages 2, 3, and 4, respectively. This figure includes experimental lots marked by removal of the adipose only, and these were affected as much as those having the severe marks. The marked fish also matured slightly later, on the average, than unmarked (Cleaver's table 14). The mean unweighted difference in years is 0.041 ± 0.103 (= SD) for the AdRM mark and 0.212 ± 0.164 for the adipose alone. The difference is nonsignificant, but we should have expected the Ad-only fish to show little or no effect. If an explanation is needed, we may note that some fish can regenerate the adipose (partly regenerated adipose fins are sometimes seen). If so, it is likely that the more vigorous and faster-growing fish would also be more successful in regeneration, so that the remainder, having nonregenerated adiposes, would be smaller and mature later. They were, in fact, smaller than unmarked fish (Cleaver's figure 3).

Ocean Tagging Method

20. Procedure — Parker (1960) described this method in detail following a summary exposition by Parker and Kirkness (1956). Data needed are as follows: 1) Tagging of salmon at sea shortly before the maturing ones set off for home waters. A range of sizes and ages should be tagged, including fish that will mature in the current year and in at least one subsequent year. If there is only a single age of maturity, as in pink salmon, the method is not applicable. 2) Recovery of tagged fish in the commercial fishery during all the years that they mature.

The conditions necessary for unbiased estimates are as follows (elaborated from Parker 1960): 1) Recoveries are made in sport or commercial fisheries only during the year that the fish are maturing. If some nonmaturing fish are caught, the estimate of natural mortality rate is too large because it includes some fishing mortality. 2) There is no noncatch mortality from the fishing operation other than immediate mortality, which is compensated for in the calculation. 3) Rate of exploitation of maturing fish is the same in all years of the experiment. 4) Natural mortality is the same for the fish of all ages and during all years of the experiment starting with the youngest age tagged. If younger fish in fact have greater natural mortality, the estimate of natural mortality obtained is too large to represent the final year of life. 5) There is no tag loss during the experiment. If loss does occur at a constant rate, it makes the natural mortality estimate too large by that amount. If losses of tags become progressively greater as time goes on, the mortality estimate is more seriously biased upward. 6) The number of tags reported each year is a constant fraction of the number caught. 7) Mortality due to catching and tagging is complete within a short time after tagging. Failure of this condition makes the natural mortality estimate too large because part of it is man-induced. 8) Mortality due to catching and tagging must be at the same

TABLE 4. Percentage of marked and unmarked chinooks that returned to the hatchery, and instantaneous rate of disappearance as observed and as reduced by a rate of fishing of 2.6. M = marked; U = unmarked. (Cleaver [1969], table 15).

		% returning		Rate of disappearance					
				Observed			Reduced by $F = 2.6$		
Hatchery	Mark	M	U	M	U	Ratio	M	U	Ratio
Spring Creek	Ad-LV-RM	0.04510	0.1636	7.704	6.415	1.201	5.104	3.815	1.338
Spring Creek	Ad-RM	0.07921	0.1636	7.141	6.415	1.113	4.541	3.815	1.190
Kalama	Ad-RV-RM	0.03278	0.08447	8.023	7.077	1.134	5.423	4.477	1.211
Kalama	Ad-RM	0.04044	0.08447	7.813	7.077	1.104	5.213	4.477	1.164
Mean						1.138			1.226

rate for all sizes of fish tagged. If smaller fish are more affected the estimate of natural mortality is too large. 9) Natural mortality must be at the same rate for tagged and untagged fish. For example, the tag must not cause a fatal lesion, nor make the fish more vulnerable to predation because the tag makes it more conspicuous than its fellows. Failure of this condition makes the natural mortality estimate too large.

Of the above, failure of conditions 3 and 6 may lead to either an overestimate or an underestimate; in general, their presence or absence cannot be predicted in advance, though it is sometimes possible to obtain ancillary information concerning them. Failure of conditions 1, 2, 5, 7, 8, and 9 all mean that the estimate of natural mortality obtained is too large. The same is true for 4 if (as is likely) younger fish have a larger natural mortality rate than older ones.

21. Chinook salmon of southeastern Alaska — Parker (1960) obtained 0.659 as an estimate of the natural survival rate of chinook salmon off southeastern Alaska. The corresponding instantaneous mortality rate is 0.417 per yr or 0.035 per mo. This applies mainly to the last 2 yr of life, but some younger fish were tagged. However, there was little information and no control on the possible sources of systematic error. Of those listed above, Parker states that 1 was not fulfilled because some fish were caught prior to the year of their maturity, and such fishing mortality would inflate the natural mortality estimate, as would any associated noncatch mortality. Failures of conditions 2, 4, 5, 7, 8, and 9 all have some plausibility, and even if no single one were very important, their combined effect could still be so. They too all tend to make the mortality estimate too large. Thus, the mortality estimate 0.035 per mo can be regarded only as a maximum value, which could easily be 2 or 3 times the actual.

DOUBLE OCEAN TAGGING METHOD

22. Procedure — Salmon of the same stock or stocks are tagged at sea on two occasions. From recaptures obtained subsequent to the second tagging, an estimate of the survival rate between the two taggings is computed.

Necessary conditions for an unbiased estimate of natural mortality are: 1) If there is mortality due to capture and the tagging process, it must be the same for the two lots of fish. 2) The presence of the tag must not make the fish either more or less vulnerable to predation than are wild fish. 3) There must be no indirect loss from fishing gear during the time between the two taggings. 4) There must be no progressive loss of tags from the fish.

23. Puget Sound cohos — Mathews and Buckley (1974) tagged cohos during two periods, using a modified Carlin tag. The first period was January 7–February 10, when the fish averaged about 32-cm fork length, and the second was May 1–June 6, when they averaged 41 cm. Recaptures made after the second tagging were compared, as follows:

	Lot 1	Lot 2
Marked	$M_1 = 169$	$M_2 = 61$
Recovered	$R_1 = 29$	$R_2 = 20$

From the large-sample formula for estimating survival rate (S) from two markings, Mathews and Buckley estimate:

$$S = \frac{R_1 M_2}{R_2 M_1} = \frac{29 \times 61}{20 \times 169} = 0.523$$

By the usual formula (Ricker 1975, p. 123) the standard error (SE) of this estimate is 0.131 from which 95% confidence limits of 0.27 and 0.78 are obtained. Mathews and Buckley give broader

limits, 0.15 to 0.89, "based on the delta method of approximation."

The survival estimate corresponds to a mortality rate of 0.648, or 0.185 per mo based on a mean 3.5-mo interval. The 95% confidence limits for the latter mortality figure are from 0.03 to 0.54 by Mathews and Buckley's method.

More important than the rather large sampling error are the possible systematic biases that affect this estimate. Mathews and Buckley made observations on troll-caught tagged and untagged chinook salmon about 30 cm long in a large aquarium over 162 days. These suggested that no tags were lost, that there was no immediate mortality due to tagging, and that the tagged fish survived as well as untagged. Large potentially predacious fish of other species were in the same aquarium, and after 2 mo the salmon gradually disappeared; however, no predation was observed, and they suggest that deaths were from starvation since the salmon did not feed. This information helps to validate condition 1 of Section 22, but it is much less satisfactory evidence concerning conditions 2 and 4. It cannot serve as a good test of differential predation because the full range of salmon predators was not present and predation was not in fact observed. Nor is the absence of tag loss in an aquarium convincing testimony that none are lost during normal active marine life.

Regarding condition 3, Mathews and Buckley state that "there was negligible fishing mortality between tagging times because most of the coho were under the minimum size limit and anglers were seeking the larger, legal-sized chinook salmon with gear and methods relatively inefficient for the small coho." No data are offered, and this opinion seems quite at variance with the evidence on shaker losses quoted in Section A. Cohos and chinooks are very incompletely separated by habitat, and while using heavier gear reduces the number of sublegal fish that are hooked it also increases the damage to those that do get hooked. Senn and Satterthwaite (1971, table 10) show that 5.72% of marked cohos of the 1966 brood from southern Puget Sound hatcheries were caught and 2.45% returned to the hatchery at age 3. If 1 coho is killed for every 2 boated, as suggested in Section 14, the shaker loss would be:

$$2.86/(2.86 + 5.72 + 2.45) = 26\%$$

of the total fish accounted for. They could make an important contribution to mortality during the period of the Mathews and Buckley experiment, which is when most coho shaker losses occur.

I conclude that much of the estimated 0.185 monthly mortality rate is due to a combination of shaker loss, progressive loss of tags, and greater vulnerability of tagged fish to predators. Consequently this figure can be used only as a maximum estimate of natural mortality rate, which may be several times too large.

Smolt Survival Method

24. Procedure — This method provides an estimate of average oceanic mortality rate, starting at some time during the 1st ocean yr. Data needed are as follows: 1) Adult returns from known smolt migrations, for as wide a range of localities and smolt sizes as possible, to establish the relation between mortality rate and size. 2) If any of the returns are of marked smolts, they must be adjusted to terms of unmarked.

The size and age at which young sockeye go to sea varies greatly between different stocks, even within a limited geographical area. Ricker (1962a, figure 1) illustrated the fact that ocean mortality rate tends to decrease as smolt size increases. He postulated that the mean annual rate experienced by the largest known smolts could serve as a standard of comparison. For any stock having smaller smolts, the standard could then represent the ocean mortality from the time during their ocean life that they achieved the size of the standard smolts. For every known stock this time occurs during the 1st yr of ocean life, or more exactly, before the first ocean annulus is laid down. The mean annual mortality rate of the standard smolts will therefore be a maximum estimate of average natural mortality during the 2nd and later years of ocean life. If it is applied to the last year only, it is very much a maximum figure because of the decrease in mortality rate as the fish become larger.

The largest known sockeye smolts are from Lake Dalnee in Kamchatka. Although natural and fishing mortality cannot be separated in available survival estimates for that stock, the observed survival rates follow the trend established by other stocks (Ricker 1962a, figure 1). Karluk Lake smolts are almost as large as Dalnee smolts, and their natural mortality was used as the standard figure by Ricker (1962a).

Fredin (1964) estimated the mortality of marked smolts somewhat differently, by using Parker's (1962b) procedure of putting all the ages at which they returned into one expression with the mortality rate. In a simple notation, his basic equation (what he called "Population Model 1") for estimating natural mortality is:

$$N = R_1e^{Mt_1} + R_2e^{Mt_2} + R_3e^{Mt_3} + \ldots \quad (1)$$

N = the number of smolts marked of a given freshwater age
R_1, R_2, etc. = the number of recoveries made in successive years of maturity, including catch and spawners
t_1, t_2, etc. = the mean time interval from marking to recovery of each ocean age-group
M = the instantaneous rate of natural mortality of *marked* smolts

The equation shows that the number of marked smolts is equal to the number of recaptures in each year divided by their respective survival rates from marking to capture (survival rate = e^{-Mt}). The equation is solved for M by trial. The mortality rate of unmarked smolts is then found by dividing M by the marking handicap ratio.

25. Karluk sockeye (Ricker's estimates) — Table 5 here is similar to Ricker's (1962a) table B, but 1.37 is used as the mark handicap ratio. The mean lengths of ocean life for the different freshwater ages are also altered slightly; the new figures were computed from the mean times at large in Fredin's (1964) table 2, combined with the returns at successive ocean periods shown in his table 3.

The mean instantaneous mortality rate for the 3-freshwater smolts is 0.036 per mo, which then is the "standard" figure, and is a maximum rate if applied to any growth period that begins at the first ocean annulus or later.

26. Karluk sockeye (Model 1 of Fredin) — Fredin's Model 1 is equal mortality rate throughout ocean life. Its estimates therefore are very similar to those in Table 5. Fredin's mean monthly instantaneous mortality estimates, divided by 1.079, are:

	No. of Expt.	Mean	SE
Freshwater age 1	4	0.0459	—
Freshwater age 2	7	0.0413	0.0019
Freshwater age 3	7	0.0358	0.0017
Freshwater age 4	7	0.0373	—

The SE for ages 2 and 3 are estimated from the variation between years. Data for ages 1 and 4 were scanty, so were lumped into a single estimate.

27. Cultus Lake cohos — Foerster and Ricker (1953) removed both ventral fins from wild coho smolts of about 14-g avg wt, trapped in Sweltzer Creek about 300 m below Cultus Lake, in 1927. Of these, 8.07% returned in 1928 to a counting fence a little below the smolt trapping site. Since the creek and lake cohos are probably incompletely separated, this represents a minimum count of age 3 adults; that is, there may have been others that did not reach or did not enter the fence traps. (Age 2 cohos also occurred, but were small enough to swim between the pickets of the 1927 fence, so no count was obtained.) No mark handicap factor is available for cohos, but the figure 1.30 can be used, being the mean of 1.37 for sockeye and 1.23 for chinooks (Sections 18 and 19). The instantaneous rate corresponding to 8.07% is 2.517, and dividing by 1.3 gives 1.94, a figure that includes fishing mortality. However, during the 1920s the troll fishery was rather small, and the Cultus cohos return to fresh water so late in the year that they missed most of the net fishery. Rate of fishing plus shaker loss would probably not have exceeded 0.5, which leaves a natural mortality rate of 1.44. Because of the probable incompleteness of the returns, this figure is likely to be somewhat too large.

The Cultus cohos are away from the lake about 18 mo, so the mean mortality rate is 0.080 per mo, again a maximum figure. The difference between this and the 0.04 per mo found for Karluk sockeye is probably mainly due to the smaller size of the coho smolts, with a contribution from the unrecorded escapement of age 2 "jacks" and possible incompleteness of the count of age 3's; but differences in habits or habitat between the two species might also play a role.

Maturity Schedule Method of Parker

28. Procedure — Parker (1962b) introduced a further elaboration into the smolt survival method by comparing different maturity schedules within the same stock, or between stocks in the same locality. The data required are: 1) Number of fish that return from at least two known smolt migrations, or from two different kinds of fish within a single migration, for which the ocean maturity schedules are different. 2) If marked fish are used in the above, an estimate of the ratio of marked:unmarked mortality rate is needed.

Parker argues as follows. (1) There is a "basic" natural mortality rate, M, applicable to the whole period of time from marking to return to fresh water. (2) During the first year there is an additional mortality, *c*, associated with estuarine and early ocean life, so that the total mortality rate during the first ocean year is M + *c*. (3) During the final year of life there may be a different mortality rate in coastal waters, so tht the total mortality rate in the final year is M + *k* (if coastal mortality is less than ocean, *k* is negative).

These postulates were inserted in equation (1)

TABLE 5. Survival rates of marked Karluk smolts and computed mortalities. The survival rates of lines 2–7 are averaged in line 8. Because of the small numbers involved, averages for freshwater ages 1 and 4 are based on the sum of marks and recoveries in all years; for freshwater ages 2 and 3 they are geometric means of the ratios for individual years. Line 10 is the instantaneous mortality rate corresponding to line 8; line 11 is the same divided by 1.37, and line 9 is the corresponding survival rate. Line 12 shows mean lengths of ocean life, and lines 13 and 14 are monthly mortality rates.

	Freshwater growing seasons			
	1	2	3	4
1. Mean fork length (*mm*)	109	132	143	150
	Survival rates			
2. 1926	0.049	0.200	0.237	0.342
3. 1929	—	0.183	0.255	0.135
4. 1930	0.025	0.166	0.280	0.325
5. 1931	0.548	0.212	0.345	0.408
6. 1932	—	0.218	0.192	0.023
7. 1933	0.188	0.183	0.259	0.156
	Mean survival			
8. Marked	0.1159	0.1930	0.2554	0.248
9. Unmarked	0.208	0.301	0.369	0.361
	Mortality rate			
10. Marked	2.155	1.645	1.365	1.394
11. Unmarked	1.572	1.201	0.996	1.018
12. Months of ocean life	31.84	28.63	27.65	27.63
	Mean monthly mortality			
13. Marked	0.0677	0.0575	0.0494	0.0504
14. Unmarked	0.0494	0.0419	0.0360	0.0368

above, giving:

$$N = R_1e^{c+k+t_1M} + R_2e^{c+k+t_2M} + R_3e^{c+k+t_3M} + \ldots \quad (2)$$

Dividing both sides by e^{c+k}, taking logarithms, and transposing:

$$c + k = \log_e N - \log_e(R_1e^{t_1M} + R_2e^{t_2M} + \ldots) \quad (3)$$

Parker then computed and plotted a series of values of $c + k$ against M, obtaining a line that was slightly curved.

Assuming that M, c, and k are the same for all the components (different year-classes and/or different freshwater ages and/or different sexes) of a given run of salmon, there can be differences between components in respect to their "maturity schedules," mainly consisting of differences in the ratio $R_1 : R_2 : R_3$ etc., and to a less extent in the ratio $t_1 : t_2 : t_3$ etc. Such differences give the lines computed from expression (3) different positions, but ideally they should all intersect at the same point, which represents the value of M and $c + k$. In practice they all intersect at different points, so mean values must be used unless there are only two lines. The value of M obtained will of course refer to the marked fish and can be adjusted to unmarked by dividing by a mark handicap factor.

The principal difficulty with this ingenious method is that in practice the computed lines often cross at points that represent negative values of M or of $c + k$. Negative M is impossible, and negative $c + k$ would indicate that coastal mortality for smolts and/or adults was less than oceanic. There is no theoretical objection to averaging all the values obtained, positive and negative, but in examples to date the large dispersion observed gives such a mean so large a sampling error as to be useless. Parker (1962b) rejected all points except those that give positive values of both M and $c + k$. This seems a commonsense approach, and there is no obvious way for it to introduce bias, but rejecting part of the available information always raises misgivings.

The sampling error of an estimate by this method depends partly on how different are the two maturity schedules being compared, and this is indicated by the size of the angle between the two lines at the point of intersection. This angle can therefore be used as a rough estimate of the relative reliability of different estimates.

29. Karluk sockeye — There are 10 lines in Parker's (1962b) figures 3–5, giving 45 possible intersections, only 6 of which lie within the range of positive values of both $c + k$ and M. It is not possible to consider all 45 intersections because they have not all been plotted on the same graph; those shown include some very large negative or positive estimates of M (at least from −1.2 to +1.1 — see Parker's figure 4).

Parker's mean estimate of M, from the 6 doubly positive intersections, is 0.262 per yr or 0.0218 per mo. This is obtained using a mark handicap factor of 1.27; adjusting to the new factor 1.37 reduces it to 0.0202 per mo. This is rather a small figure, considering that on the hypothesis used it applies to most of the fish's ocean life, starting from some time in the first ocean growing season. The mean estimate of coastal mortality, similarly adjusted, is 0.511. The SE for the mortality rate 0.0202 is 0.0039, based on the 6 doubly positive intersections. The SE for a mean of values from all the intersections would be much greater, even though the increased dispersion is partly compensated by the larger number of observations.

30. Cultus Lake sockeye — Figure 7 of Parker (1962b) has only 1 pair of lines, hence only one intersection. The 2 lines meet at such a small angle that the precision of the estimate obtained is extremely low. The estimate is 0.0388 per mo, which can be adjusted to 0.0360, but the value is too uncertain to be useful.

31. Lake Dalnee sockeye — Parker's (1962b) figure 6 shows that only 3 intersections out of a possible 45 give positive values of M and $c + k$. These indicate an average M of 0.344 per yr or 0.0287 per mo, which can be adjusted to 0.0267 per mo using the new mark handicap factor. This rate includes some fishing mortality, so it is a maximum estimate of natural mortality.

32. Hook Nose Creek sockeye — Parker (1962b) drew lines for 2 yr and both sexes, and the male sex was further divided on the basis of two estimates of the fishing mortality rate on the 2-ocean fish (jacks). However, the rate of fishing on even the 3-ocean fish was quite uncertain: it was estimated from "the general level of catches and escapements in the general area," and Parker (1962a) showed that in the case of pink salmon the general estimate was far from being representative of Hook Nose Creek. Another uncertainty is the use of a 50 : 50 sex ratio for sockeye smolts; Parker quotes an actual estimate of 51.69% males at Hook Nose in 1949, and Ricker (1975, p. 201) reviews evidence that a small excess of males is the usual situation among young salmon.

Considering everything, it is impossible to attach any weight to the average mortality figure quoted by Parker, which is 0.030 per mo when adjusted to a 1.37 mark handicap ratio.

33. Hook Nose Creek pink and chum salmon — Figure 9 of Parker (1962b) shows one pair of lines for the pink–chum comparison, which meet at a satisfactorily wide angle to give a natural mortality estimate of 0.231 per yr or 0.019 per mo, using a mark handicap ratio of 1.52 (Section 17).

In this comparison of pinks and chums there is the assumption that they suffer the same ocean mortality rate, this being considered constant throughout ocean life (apart from the coastal mortality). On the hypothesis that mortality is a function of size this is not tenable, because chums are much larger than pinks at maturity and hence, also during much of their ocean life. With the failure of this assumption no unbiased estimate is possible; its effect is to make the estimate too large. The figure 0.019 per mo must therefore be considered a maximum.

Mortality Distribution Method

34. Procedure — This is an extension of the Smolt Survival Method, in which an observed total mortality rate is divided up by months according to some hypothesis relating to the change in mortality with age or size. Fredin (1964) proposed three such hypotheses (his Models 2, 3, and 4), and applied them to the Karluk sockeye. Two other models are used in the Inverse Weight Method and the Comparison of Mortalities Method, both presented later.

35. Karluk sockeye (Model 2) — In Fredin's (1964) Population Model 2 monthly instantaneous mortality rates are made to decrease by a fixed quantity per month, until after 48 mo they are reduced to zero, and the initial value is chosen so that this will be so. The computation is made by inserting appropriate factors into successive exponents of expression (1). Divided by 1.079, the values obtained by Fredin are as follows:

	Initial	Monthly reduction
2-Freshwater	0.0602	0.00126
3-Freshwater	0.0509	0.00106

This schedule is more realistic than Model 1, but during the last few months the rate of reduction is too precipitous to be likely.

36. Karluk sockeye (Model 3) — In Fredin's (1964) Population Model 3 the mortality rate is made to decrease rapidly during the first 6 mo of ocean life, and remains steady thereafter. While this is an improvement over Model 1, it requires an arbitrary estimate of mortality during most of the ocean life of the fish, so it really sheds no new light on this part of the life history. The chosen steady levels of monthly mortality rate, divided by 1.079 were as follows:

2-Freshwater	0.0141
3-Freshwater	0.0120

37. Karluk sockeye (Model 4) — In Fredin's (1964) Population Model 4 it is postulated that 2-freshwater and 3-freshwater sockeye have the same natural mortality rate after their 1st mo of ocean life, and that the 1st-mo mortality rate of 3-freshwater sockeye is 20 times as large. From these assumptions and observed returns the magnitude of the 1st-mo mortality of both types of sockeye can be computed, as well as the common survival rate of later months. There are 7 experiments providing 7 sets of mortality estimates whose average results, divided by 1.079, are as follows:

	Mean	SE
1st mo, 2-Freshwater	0.6067	0.0464
1st mo, 3-Freshwater	0.4307	0.0230
Subsequent mo	0.0215	0.00115

This method includes two hypotheses and an arbitrary numerical assumption. The first hypothesis is that natural mortality rate is constant after the 1st mo of ocean life, whereas we expect it to decrease with time. The second hypothesis is that 2-freshwater and 3-freshwater smolts have the same mortality rates after the 1st mo of ocean life, whereas we expect the 2-freshwater fish to experience greater mortality because of their smaller size (Section 58). The effect of this assumption is to magnify the estimate of the difference in mortality between the two kinds of smolts in their 1st ocean mo. Finally, the value 20 : 1 chosen for the ratio of 1st-mo to later-months' mortality appears to be arbitrary, so that there would really be no objective basis for the estimates shown above even if the two hypotheses were valid. However, they explore one field of possibilities.

Comparison of Life Histories Method

38. Procedure — Consider two salmon stocks (or subdivisions of stocks), A and B, which spawn in the same stream and have similar freshwater life histories, but which differ in the number of years they spend in the ocean — stock A having the longer ocean sojourn. Parker (1962a), who introduced this method, applied it to stocks of pink and chum salmon inhabiting the same stream, but it can also be applied to different ocean types of the same species. Let Y_A represent the mean number of eggs per fish (both sexes) in the spawners of stock A. If the stock is maintaining itself, i.e. is reproducing itself with no sustained trend in abundance either up or down, its mean survival rate is $1/Y_A$ and its mean total instantaneous mortality rate for the whole life history is $-\log_e(1/Y_A) = \log_e Y_A$. Similarly the total instantaneous mortality rate for stock B is $\log_e Y_B$. Total instantaneous mortality rate can be divided into freshwater mortality (W), ocean mortality (M), and fishing mortality (F). Thus the difference between the ocean mortalities of stocks A and B is:

$$M_A - M_B = (\log_e Y_A - \log_e Y_B) - (W_A - W_B) - (F_A - F_B) \quad (4)$$

Obviously to estimate $M_A - M_B$ from fecundities the following conditions must be met: 1) Either $W_A = W_B$ or their difference is known. 2) Either $F_A = F_B$ or their difference is known.

39. Hook Nose chum salmon — Parker (1962a) used data of Neave and of Hunter (1959) for the pink and chum salmon of Hook Nose Creek, King Island, B.C. Mean fecundity per adult (both sexes) was 850.8 eggs for pinks and 1269 for chums. Consequently the total mortality rates are $\log_e 850.8 = 6.746$ for pinks and $\log_e 1269 = 7.146$ for chums. Then assuming $W_A = W_B$ and $F_A = F_B$ in expression (4), Parker estimated the instantaneous natural mortality rate for the chums' 2 extra yr of ocean life as $7.146 - 6.746 = 0.400$. This is 0.200 per yr, or 0.0167 per mo.

Regarding the assumption $W_A = W_B$, although the freshwater lives of the two species are not completely synchronized (chum adults entered the creek, and the fry left it, 2 to 3 wk later than pinks), there was a large correlation between the fry survival rate of the two species in the same year. The actual survival figures in Parker's table 1 can be converted to instantaneous mortality rates and averaged, giving 2.572 for chums and 2.556 for pinks — which is of course a non-significant difference. Subtracting these from the total mortality rates above leaves 4.574 for chums and 4.190 for pinks; this reduces the estimate of ocean mortality rate to 0.384 per 2 yr or 0.0160 per mo. Parker made the same computation on the basis of the total eggs and total fry produced during the 14 yr and obtained mortality rates

TABLE 6. Number and mean weight of mature eggs in Skeena sockeye of the same brood that spend 3 and 4 growing seasons, respectively, in the ocean. C, females taken in the catch; E, females in the escapement; GM, geometric mean. (Bilton [1970], table 2.)

		No. eggs/female			Mean wt of an egg (*mg*)			Product of ratios
Year-class	Sample	3-ocean	4-ocean	Ratio	3-ocean	4-ocean	Ratio	
1958	C	3038	3675	0.827	151	171	0.883	0.730
	E	2750	3387	0.812	142	162	0.877	0.712
1959	C	3115	3554	0.876	153	167	0.916	0.803
	E	2793	3207	0.871	143	156	0.917	0.799
1960	C	2984	3333	0.895	149	160	0.931	0.834
	E	2607	2997	0.870	138	150	0.920	0.800
1961	C	2934	3610	0.813	148	169	0.876	0.712
	E	2645	3285	0.805	139	159	0.874	0.704
GM				0.845			0.899	0.760

of 2.612 chums and 2.462 for pinks, the difference being 0.150. This adjustment reduces the estimate of 2-yr ocean mortality to 0.250, or 0.0114 per mo. It is debatable which of these two figures we should use, or whether we should, following Parker, disregard both and assume that the freshwater survival rates were equal. In any event, the figures suggest that Parker's mortality estimate of 0.0167 per mo may be somewhat too large rather than too small.

For the assumption that $F_A = F_B$ the evidence is only that both pink and chum salmon are caught in the same kind of gear. Obviously this is not a guarantee of an equal rate of fishing, especially when the chums are larger and run 2–3 wk later than the pinks (Hunter 1959). Thus, the natural mortality estimate 0.0167 per mo may have a systematic bias whose magnitude and direction are both unknown.

40. Babine sockeye — The sockeye of Babine Lake spend either 3 or 4 growing seasons (including part seasons) in the ocean. The two types are approximately equal in numbers on the average, though variable from year to year. (Sockeye having only 2 ocean growing seasons or more than 4 ocean growing seasons also occur but are scarce enough that they usually contribute little to reproduction.) The longer time at sea means that the older fish become larger, and they produce more and somewhat larger eggs. On the other hand, they are reduced in numbers by natural mortality during their extra year at sea. The effects of these two factors upon reproductive potential should be the same, on the average, for otherwise the ocean age group that produced fewer progeny would gradually disappear from the stock. Length of ocean life is partly under genetic control and can be changed by selection (Ricker 1972).

Bilton (1970, table 2) gives the mean number of eggs and mean weight of eggs of 1-freshwater Skeena sockeye of the year-classes 1958–61, shown here in Table 6. Bilton gives figures for eggs in both the catch and the escapement, because for both ocean age categories the fish caught are of a larger average size and fecundity than those that escape the nets (Larkin and McDonald 1968; Todd and Larkin 1971).

The geometric mean of the eight egg-count ratios in Table 6 is 0.845.

Using the hypotheses that $W_A = W_B$ and $F_A = F_B$, expression (4) estimates the GM survival rate in the final year of life of 4-ocean Skeena sockeye as 0.845; the corresponding mortality rate is 0.155; and the instantaneous mortality rate is 0.168 per yr, with a standard deviation (SD) of 0.043. This is equivalent to 0.014 per mo.

Considering first the assumption that $W_A = W_B$, it requires that 3-ocean and 4-ocean fish occur in the same local spawning stocks of the system (as is true at Babine Lake according to Hanson and Smith 1967), rather than merely in the system's run as a whole. For if the two types used different spawning grounds, we would suspect that age and egg size had become adapted to local characteristics of gravel size, available oxygen, and so on. A second possible cause of bias is less easily disposed of. It can be argued that the eggs of the 4-ocean fish should produce more viable fry, perhaps in proportion to their mass, in which case the estimate of final-year ocean survival rate is 0.760 (Table 6), and the corresponding mortality rate is 0.023 per mo. However, it is also possible that a larger egg is at some disadvantage in respect to respiration if

there happens to be a critical level of dissolved oxygen in the redd, and we might expect natural selection to have made the overall mean egg size an optimum for the kind of substrate in the redds used by each stock. Thus, it is not certain that larger egg size confers an overall advantage in freshwater survival.

The second assumption used above is that rate of fishing on sockeye of the two ocean ages is the same. This is not correct: a larger fraction of the larger sockeye is caught than of the smaller ones, and since 4-ocean fish average somewhat larger than 3-ocean, it follows that $F_A > F_B$ (Larkin and McDonald 1968; Todd and Larkin 1971). Unfortunately it seems impossible to estimate the magnitude of $F_A - F_B$, except to say that it must be quite appreciable, because the average value of F for all Skeena sockeye in recent years has been 0.7–0.8, and formerly it was larger (Ricker and Smith 1975). The effect of assuming $F_A = F_B$ is then to make the estimate of ocean mortality rate from (4) too large. This bias tends to compensate for the effect of any bias due to difference in freshwater mortality ($W_A < W_B$), discussed in the previous paragraph.

Maturity Schedule Method of Fredin

41. Procedure —Data needed are as follows: 1) Information on the number of fish of a given year-class and freshwater age that return from the sea in 2 successive yr, for example, $R_{1/3}$ in year 1 and $R_{1/4}$ in year 2. 2) The fraction of maturing fish among the salmon of a given freshwater age present in the ocean on May 1 of year 1, that is, before the shoreward migration of the maturing fish begins. For the above group this fraction is represented by $p_{1/3}$.

The principal condition necessary is that the 3-ocean fish should have the same natural survival rate between May 1 and the time they are caught or reach the spawning ground in year 1, as do the 4-ocean fish during the same interval of year 2. Fredin (1965, p. 47) quotes direct evidence from tagging that these rates were much the same in a given year.

Let the survival rate of immature 1-freshwater fish between May 1 of year 1 and May 1 of year 2 be S_1. Then Fredin shows that:

$$S_1 = \frac{R_{1/4}p_{1/3}}{R_{1/3}(1 - p_{1/3})} \tag{5}$$

Similarly the survival of 2-freshwater fish for the same period is:

$$S_2 = \frac{R_{2/4}p_{2/3}}{R_{2/3}(1 - p_{2/3})} \tag{6}$$

42. Bristol Bay sockeye — Fredin (1965) applied his maturity schedule method to Bristol Bay sockeye, using age characteristics of the runs of 1958 and 1959. To estimate the fractions $p_{1/3}$ and $p_{2/3}$ he used the natural mortality distributions indicated by three of the population models postulated for Karluk sockeye (Fredin 1964), namely Models 1, 3, and 4 (see Sections 26, 36, 37). All of these assume a constant natural mortality after the 1st ocean winter. Unfortunately the estimate of S is quite sensitive to the values chosen for p, so any estimate obtained in this way is bound to have a considerable element of arbitrariness. Fredin used the mean of the average percentages maturing obtained from the three models mentioned, but we must reject Model 1 (uniform natural mortality rate from smolt to adult) as far too unlikely. Population Models 3 and 4 give an average $p_{2/3}$ value of 0.598; applying this in expression (6):

$$S_2 = \frac{0.787 \times 0.598}{1.485(1 - 0.598)} = 0.788$$

This corresponds to an instantaneous mortality rate of 0.238 per yr or 0.0198 per mo. However reasonable this may seem, the assumptions required for the estimate of $p_{2/3}$ mean that it adds little to our quantitative understanding of natural mortality.

Ocean Immatures Method

43. Procedure — This method, invented by Fredin (1965), requires the following information: 1) The number of adults that return from two successive smolt migrations as 3-ocean fish ($R_{3\cdot3}$ and $R_{3\cdot4}$) and as 4-ocean fish ($R_{4\cdot4}$ and $R_{4\cdot5}$). (The first subscript designates ocean age and the second is the calendar year of maturity, given that the first smolt migration occurred in year 1.) 2) An estimate of the ratio $I_{2\cdot3}/I_{1\cdot3}$, which is the relative number of immature sockeye that have completed 2 and 1 ocean growing seasons, respectively, that are present in the sea during the summer of year 3. In the only application of the method to date, this estimate came from purse-seine catches in the open sea.

Fredin developed the above information into an expression for the survival rate S_0 during the penultimate year of life of 4-ocean sockeye, or more exactly, from August 1 of year 2 to August 1 of year 3, given that the smolt migration occurred in year 1. By combining Fredin's expressions (12) and (13) this can be written as follows:

$$S_0 = \frac{R_{4\cdot5}I_{2\cdot3}/I_{1\cdot3}}{R_{4\cdot4} - R_{3\cdot4}I_{2\cdot3}/I_{1\cdot3}} \tag{7}$$

Conditions required for accuracy of this method are: 1) The observed ratio $I_{2\cdot3}/I_{1\cdot3}$ must really represent the relative abundance of 2+ ocean and 1+ ocean immature fish in the sea at that time. 2) The survival rate during the last year of ocean life should be the same for sockeye designated as 3-ocean and 4-ocean, respectively, when mature.

44. Bristol Bay sockeye — From published sources Fredin (1965) made estimates of the number of 3-ocean and 4-ocean fish that mature each year, including those taken by high-seas and coastal fisheries and the escapement. The relative number of 1+ ocean and 2+ ocean sockeye at large on August 1 of each year was indicated by the number captured in Hartt's seining south of Adak. Computations can be made for 5 pairs of years; however, Fredin lumped the data for all 5 and obtained 0.805 as the combined estimate of survival rate during the penultimate 12 mo of life of 4-ocean fish; this is an instantaneous mortality rate of M = 0.217, or 0.018 per mo.

To get an idea of the sampling error of this figure, I computed estimates of S_0 for the 5 pairs of years separately, as follows: 0.888, 0.446, 0.369, 0.942, and an indeterminate figure of which it can be said only that it is greater than 1. Using 1 for the last value, the mean of these 5 is 0.729 and their SD 0.297. The SE of the mean is, therefore, $0.297/\sqrt{5} = 0.133$. A figure somewhat larger than this, say 0.15, could serve as an estimate of the SE of the combined survival rate of 0.805. The 95% confidence limits for S would therefore be $0.805 \pm 2.776 \times 0.15$, or from 0.389 to 1.221; the corresponding limits for the natural mortality estimate M = 0.217 per yr are from 0.94 to beyond 0.

Although its sampling error is large, there is no appreciable source of bias in this estimate. The representativeness of the Adak catches was tested by Fredin by plotting R_3/R_4 against I_1/I_2 for 6 pairs (his figure 1). The correlation coefficient was 0.91 and, more important, the distribution of the points agrees well with the hypothesis of direct proportionality, which would be represented by a straight line through the origin. As regards condition 2 above, Ricker (1962a, tables B and C) shows that for sockeye of a given freshwater age, the difference in final size between 3-ocean and 4-ocean individuals can vary from 0 up to 500 g. However column 4 of Table 7 indicates that weight differences of this order in the last year of life make almost no difference to the mortality rate. And as mentioned in Section 41, Fredin had direct evidence from tagging that the 2 rates do not differ significantly: there were 22.9% returns of tags from 3-ocean fish and 24.8% from 4-ocean fish tagged 1–2 mo prior to the fishery, and a difference in this direction would be expected because tag returns were mostly from the catch, and the 4-ocean fish, which are larger, are probably more vulnerable to the gillnets used.

Smolt Indices Method

45. Procedure — Another product of Fredin's (1965) inventive mind, this method requires data as follows: 1) The number of smolts (N) that migrate to sea in at least 2 successive yr. 2) The number of these that return as 3-ocean fish (R_3) and the number that return as 4-ocean fish (R_4) — including both catch and escapement. Two-ocean and 5-ocean mature fish are presumed to be negligible, but if not, an adjustment can easily be made.

Conditions involved include: 1) The survival rate of the 3-ocean spawners, during the approximately 2 yr from smolt migration to the time they start to return to coastal waters, should be the same as that of the 4-ocean spawners during the same 2 calendar yr. 2) If there is a different rate of "coastal" mortality toward the end of the life history, it affects 3-ocean and 4-ocean spawners equally.

Let the survival rate from smolt migration to the time of return to the coast of 3-ocean fish be S. Let p be the fraction of those alive in the spring of the 3rd ocean yr that mature as 3-ocean fish. Let S_4 be the survival rate of the 4-ocean fish during their final year (approximately) of ocean life. The above is described by two equations:

$$R_3 = NpS \tag{8}$$

$$R_4 = N(1 - p)SS_4 = NSS_4 - NpSS_4 \tag{9}$$

Substituting (8) in (9):

$$R_4 = NSS_4 - R_3S_4 \tag{10}$$

This is a linear equation in R_4 and R_3, which can be solved directly for S_4 and NSS_4 if 2 yr data are available. If more than 2 yr are available, R_4 can be plotted against R_3 and a straight line fitted; its slope is an estimate of S_4, and the Y-axis intercept is an estimate of NSS_4, from which S can be calculated. Since R_3 and R_4 are equally subject to sampling error, a functional line must be used (Ricker 1973).

Either marked or unmarked smolts can be used in an estimate of this type. If the former, the survival rates and corresponding mortality rates must be adjusted to terms of unmarked (Section 18). Also, the returns used (R) can be either the escapement alone, in which event S_4

includes the effect of the fishery, or catch plus escapement, when S_4 will estimate natural mortality only.

Bias in this estimate is likely to arise from the failure of condition 1, the assumption that the survival rate S is the same for spawners having 2 and 3 ocean yr, respectively. It is usual for larger fish to mature earlier; this is shown, for example, in Lander and Tanonaka's (1964) figures 16 and 17. Accordingly we expect the future 4-ocean fish to have a larger mortality rate than the future 3-ocean fish during the first 2 yr of ocean life of both.

In any given run 2-freshwater fish are larger than 1-freshwater fish, and 3-freshwater fish are larger than 2-freshwater, during at least their first 2 yr of ocean life, so their mortality rates should also be different. For this reason Fredin (1965) was able to reduce the above difference in size and in mortality rate between the two ocean types by working with fish of a single freshwater age, but considerable difference would remain even within this restricted group. To find the effect of this difference, let S′ be the survival rate of the 4-ocean fish involved in equation (10), and S that of the 3-ocean fish, during their first 2+ ocean years; $S > S'$. Then expression (10) becomes:

$$R_4 = NS'S_4 - R_3S_4S'/S \qquad (11)$$

and the computed value of S_4 will be too small if the factor S'/S is ignored.

46. Karluk sockeye — Fredin (1965) obtained an estimate of 0.657 for the survival rate of marked sockeye during their 3rd "yr" (actually 10.67 mo) of ocean life, with the large SE of 0.826. This corresponds to an instantaneous mortality rate of 0.42 per yr, which was adjusted using the factor 1.27 to 0.33, or 0.031 per mo. The revised mark handicap ratio 1.37 makes this 0.029 per mo.

However the survival rate 0.657 was computed from an ordinary regression of R_3 on R_2. The GM functional regression gives an estimate of 1.78, with 95% confidence limits of 0.610 and 5.19 (Fig. 1). The bias indicated in equation (11) would make the true estimate somewhat larger; however, it is already greater than unity, or 100% survival, so no useful estimate is obtained.

Dichotomy and Maturity Schedule Method

47. Procedure — In this method Mathews (1968) makes use of the "change in composition" or "dichotomy" method of censusing populations (Murphy 1952; Chapman 1955). Data

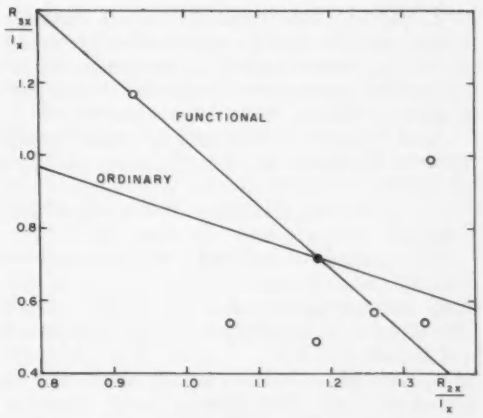

FIG. 1. Regression of 3-ocean spawners on 4-ocean spawners (each divided by the same constant), in Fredin's example of the smolt indices method. Two different regression lines are shown (see the text).

required are: 1) Catch and escapement of two freshwater ages of salmon in 3 successive yr. 2) Estimates of the relative abundance of immature fish of the two freshwater ages in the ocean in 2 successive yr.

The principal conditions required are: 1) Different percentages of the two freshwater ages must mature after successive periods of ocean life. 2) The natural mortality rate of fish of a given ocean age must be independent of their freshwater age. Specifically, the mean natural mortality rate for all 1-freshwater fish must be the same as the mean for all 2-freshwater fish.

The computation makes use of the change in the fraction of 2-freshwater sockeye in the ocean resulting from different fractions of the 1- and 2-freshwater groups maturing after 3 ocean yr. These ratios are estimated from high-seas catches.

A simplified list of symbols is shown below, with the numerical values used in Mathews' Bristol Bay example shown in parentheses:

P_1 the ratio of 2/1+ to (2/1+ plus 1/1+) sockeye present in the ocean during the summer of year 1. This is assumed to be the same as, and is used as an estimate of, the ratio of 2/2+ to (2/2+ plus 1/2+) in year 2 before the departure of maturing 3-ocean fish that year (0.902).

P_2 the ratio of 2/2+ to (2/2+ plus 1/2+) sockeye during the summer of year 2 after maturing 3-ocean fish have departed (0.747).

S_1 the ocean survival rate between 1+ ocean immature sockeye on July 1 of year 1 and 2+ ocean sockeye on June 30 of year 2, assumed to be the same for 1-freshwater and 2-freshwater fish.

S_2 survival rate from 2+ ocean immature sockeye on July 1 to 3+ ocean maturing sockeye (= 4-ocean when mature) in the fishery and the escapement, assumed to be the same for the two freshwater types.

N_1 the number of immature 1+ ocean sockeye (of both freshwater ages) in the ocean on July 1 of year 1.

N_2 the number of immature 2+ ocean sockeye present in the ocean on July 1 of year 2.

J the number of immature sockeye caught on the high seas in year 2 (0.561 million).

R_1 the number of mature 1/3 sockeye in the run of year 2, including catch and escapement (1.388 million).

R_2 the number of mature 2/3 sockeye in the run of year 2 (54.409 million).

R_3 the number of mature 1/4 and 2/4 sockeye in the run of year 3 (15.007 million).

The number of sockeye present in the sea just prior to the shoreward migration of maturing fish in year 2 is estimated from the dichotomy formula as:

$$N_1S_1 = \frac{R_2 - p_2(R_1 + R_2)}{p_1 - p_2} \quad (= 82.123) \qquad (12)$$

After the spawning run of year 2 has departed, the above number is reduced to:

$$N_2 = N_1S_1 - (R_1 + R_2 + J) \quad (= 25.765) \qquad (13)$$

In year 3 all the remaining fish mature and they number R_3. The survival rate of these fish in their last 12 mo of life is therefore:

$$S_2 = \frac{R_3}{N_2} \quad (= 0.582) \qquad (14)$$

Unfortunately it turns out that this method is sensitive to small departures from condition 2 above. This is illustrated in the example below.

48. Bristol Bay sockeye — Mathews (1968) used data from Hartt's (1959, 1962) high-seas sampling south of Adak to represent the life-history types of immature Bristol Bay sockeye present in the ocean in 2 successive yr. He found that in all the years of this sampling there was only one set of 2 successive yr that was suitable — 1964 and 1965. The data are shown with the symbols and equations above. The survival estimate is $S_2 = 0.582$, from which the natural mortality is 0.541 per yr or 0.045 per mo. Mathews computed 95% confidence limits for this figure of 0.028 — 0.064. However, these are based on random sampling theory, and do not take into account the other sources of variability that haunt such estimates. Limits based on actual replication would undoubtedly be much broader.

But no matter what its sampling error, the figure 0.045 per mo can be considered only as a maximum estimate of natural mortality. Its bias arises from the failure of condition 2. Quoting Mathews (with the numerals changed to our notation), this condition is that "all 1+ ocean sockeye are assumed to be exposed to the same average rate of mortality, and all 2+ ocean immatures are likewise assumed to be subject to a common average rate, which may differ from that experienced by 1+ ocean fish." But 1-freshwater immature sockeye are smaller than 2-freshwater immatures at the time when both have 1+ to 2+ yr of ocean growth. Several examples of this are given by Ricker (1962a, appendix 1), but the best information for the present purpose is given by French et al. (1976, figures 37 and 38). Sockeye caught in the open ocean near Adak, having one ocean annulus, had the average lengths in centimeters shown below; the cubes of the lengths are also shown, these being approximately proportional to weight:

	1-Freshwater	2-Freshwater	Ratio
1968 (L)	34.4	35.9	
1968 (L^3)	40,710	46,270	0.880
1969 (L)	34.6	36.7	
1969 (L^3)	41,420	49,430	0.838

The best comparison is between fish of the same year-class: the ratio of the weight of 1968 1-freshwater fish to that of 1969 2-freshwater fish is 40,710/49,430 = 0.824; the within-year comparisons give similar but slightly larger figures.

In line with Mathews' view that survival rate is approximately proportional to weight (see Section 56), assume that the survival rate of the 1-freshwater fish was 0.824 of that of the 2-freshwater fish. The 2-freshwater fish amounted to $p_1 = 0.902$ of the total immatures early in their 2nd ocean summer, so that for every 902 2-freshwater individuals there were 98 1-freshwater. During the ensuing year this ratio alters so that for every 902 2-freshwater there are $0.824 \times 98 = 80.8$ 1-freshwater. The fraction of 2-freshwater fish early in the third summer is therefore $902/(902 + 80.8) = 0.918$, and this value must be used instead of 0.902 in equation (12). This gives:

$$N_1S_1 = (54.41 - 0.747 \times 55.80)/(0.918 - 0.747) = 74.43$$
$$N_2 = 74.43 - 56.36 = 18.07$$
$$S_2 = 15.01/18.07 = 0.831$$
$$M = -\log_e 0.831 = 0.186 \text{ per yr, or } 0.016 \text{ per mo}$$

Thus, a small difference in survival rate between the 1-freshwater and 2-freshwater fish has reduced the estimate of monthly natural mor-

tality rate in the final year of ocean life from 0.045 to 0.016. The revised estimate is similar to that from other nonbiased methods, but its sampling error is obviously large.

Limit-Mean Method

49. Procedure — Lander (1973) proposed this method for marked smolt experiments in which a central unbiased estimate is not available. An upper and a lower limit are computed for the estimate of mortality rate, using several assumptions. If there is no ocean catch, two assumptions suffice: 1) Natural mortality rate is larger during the interval between smolt and first age of maturity than it is later. 2) Natural mortality rate after the first age of maturity, among the fish that remain in the ocean, is greater than zero.

If there is a known ocean catch additional assumptions are needed, and the argument becomes complex. However, on the basis of these assumptions Lander computes upper and lower limits for "natural" survival rate from smolt to adult, and uses their geometric mean as the estimate. This estimate includes the noncatch mortality associated with ocean fishing operations.

50. Columbia River cohos — Lander and Henry (1973) apply the limit-mean method to get estimates of natural and ocean fishing mortality for Columbia River marked hatchery-reared cohos. Here M_1' represents the mean instantaneous noncatch mortality rate from smolt release in the spring to the time the 1-ocean fish ("jacks") return in the fall, a period of about 6 mo. M_2' is the mean noncatch mortality rate from that time to the return of 2-ocean fish 12 mo later. The symbol M′ is used instead of M because they include all sources of noncatch mortality in the ocean. An adjustment for mortality caused by marking is included in Lander and Henry's data, but they give no details. They estimate the instantaneous rates of noncatch mortality (their "natural" mortality) and of fishing mortality as follows:

	1965 brood	1966 brood	Mean
Fishing mortality (F)			
Per month	0.332	0.300	0.316
For 4.5 mo season	1.494	1.350	1.422
Noncatch mortality (M_2')			
Per month	0.0644	0.0613	0.0628
For 12 mo	0.773	0.736	0.754
Noncatch mortality (M_1')			
Per month	0.403	0.386	0.395
For 6 mo	2.418	2.316	2.367

Apart from the potential bias — unknown as to magnitude or direction — that exists in a limit-mean estimate, the experiments described in Section A show that much of the "natural" mortality in the estimates above is shaker loss caused by the fishery. Heaviest shaker losses occur in spring before the coho season opens on June 15, and there is also some loss of "grilse" the previous summer and autumn. Even during the coho commercial season a considerable number of fish escape the hook and some of them die, while others are removed by sharks, etc. With a rate of fishing as large as 1.42, corresponding to 76% removal, this effect can be appreciable. These losses must greatly inflate M_2, and have some effect on M_1. For example, if during the last year of life of the 2-ocean cohos, 1 fish dies from noncatch fishing mortality for every 3 boated, this component of the mortality M_2' is about 0.47, leaving 0.28 or 0.23 per mo for true natural mortality. If the proportion is 1 dead for 2 boated, the true natural mortality becomes 0.002 per mo, which is probably unrealistically small. The main point is that the mean M_2' value of 0.063 per mo for these cohos does not conflict with a value in the range $M_2 = 0.01$–0.02 per mo for true natural mortality.

Taguchi's Method

51. Procedure — Taguchi (1961b) developed a very ingenious set of equations that, along with sufficiently precise data for Asian salmon, could provide estimates not only of natural mortality rate (M_0), but also the rate of offshore fishing (F_0), the rate of escape of temporarily-entangled fish from offshore gillnets (F_1), and the rate of mortality among those escaped fish due to the fact they had been in the net (M_1). The information required is 1) the size of the offshore catch (C) and the coastal catch (C_1) in numbers; 2) the duration of the offshore fishery; 3) the mean time elapsed from the offshore fishery to the time the fish reach Soviet coastal fisheries; 4) the rate of exploitation by coastal fisheries (f); 5) the fraction of net-marked fish in coastal fisheries — this is to indicate the proportion of fish caught there that have escaped the offshore nets and survived to reach the coast; 6) the ratio R/R_1, where R is the abundance of the coastal stock when offshore fishing exists, and R_1 is its abundance in the absence of offshore fishing; and 7) the combined instantaneous rate of mortality, among fish that have been entangled in but escape from the offshore nets, due to natural causes and due to the effects of being caught and escaping ($M_0 + M_1$).

The reliability of the data used will be dis-

cussed briefly under the individual species. In general, however, if the quantity of interest to us here (M_0) is small relative to the other causes of death involved in the equations (M_1, F_0, F_1 and f), it would seem unlikely that any reliable result could be obtained.

52. Chum salmon — The data used by Taguchi (1961b) are as follows:

Mean offshore catch in 1957–59 — 17.3 million
Mean coastal catch — 7.88 million
Duration of offshore fishery — 50 days
Mean time from the end of the offshore fishery to the coastal fishery — 50 days
Coastal rate of exploitation (f) — 0.5–0.6
Fraction of net-marked fish — 0.15
R/R_1 — 0.65
$M_0 + M_1$ — 0.0197 per day

Although few details are given concerning any of these figures, and all have some degree of uncertainty, the least reliable items evidently are f and $M_0 + M_1$. The latter is estimated from recaptures of chums caught in gillnets and tagged near the Kuril Islands in 1935–37, combined with a probably unreliable figure (10.2%) for the rate of exploitation in the coastal fishery at that time; the latter was based on fish tagged near the coast without any evaluation of the effects of the tag or of incomplete recovery. But whether reliable or not, these data have nothing directly to do with the fate of untagged chums that escaped the high-seas gillnets in postwar years.

The coastal rate of exploitation (f) is based only on information for the west Kamchatkan Ozernaya run of *sockeye* in 1951–59 (details not given), so applying it to chum salmon along the entire littoral of the Sea of Okhotsk represents a doubly uncertain extrapolation. There is also a curious contrast between the value 0.5–0.6 for 1951–59 and the 0.102 for 1935–37 mentioned above. We should have expected the difference to be in the other direction, because in 1951–59 coastal fishing was being reduced to compensate for the high-seas fishery, whereas before the war the great bulk of the (much larger) catch came from the coastal fisheries.

By varying the above data within reasonable limits it is easy to obtain impossibly large values of M_0 as well as impossibly small ones — negative in fact. Taguchi's figures give $M_0 = 0.0119$ per day for $f = 0.5$ and $M_0 = 0.0135$ for $f = 0.6$. Both are impossibly large. For example, we should expect natural mortality earlier in ocean life to be at least no less than what it is during the last 100 days. If the mean of the above values is applied to the whole of the average ocean life of an Asian chum salmon, say 1200 days, the total instantaneous mortality rate is 15 and the survival rate is 0.000,000,3. Yet chum salmon average no more than 4000 eggs per female, which means that even without any freshwater mortality the ocean survival rate must be $1/2000 = 0.0005$ to maintain the stock. Given 10% freshwater survival this becomes 0.005, and the corresponding mortality rate is 5.3 or 0.0044 per day — which is an approximate upper limit for possible values of M_0.

Overestimation of M_0 also means that Taguchi's estimate of the rate of fishing mortality on the high seas ($F_0 = 0.0077$–0.0082 per day, or 0.38–0.41 for a 50-day fishing season) is too small, and his estimate of the size of the stock is too large.

53. Sockeye salmon — Taguchi (1961c) applied the same method to the sockeye of western Kamchatka, using the following data:

Mean offshore catch — 6.60 million in 1957–59
Mean coastal catch plus escapement (R) — 1.92 million
Duration of offshore fishery — 50 days
Mean time from offshore fishery to coastal fishery —30 days
Mean rate of exploitation — 0.34; however, the values of R were estimated for each year separately and were averaged as shown above
R/R_1 — 0.465
$M_0 + M_1$ — 0.0374 per day

These figures have most of the same weaknesses as those for chum salmon, and are said by Taguchi to be less reliable on the whole. He estimates $M_0 = 0.023$ per day, again a completely impossible figure. Parker (1963) has criticized this estimate in detail.

Cleaver's Method

54. Procedure — This method is described by Cleaver (1969) and Henry (1971, 1972). It does not provide any unique estimate of natural mortality, but it is convenient to consider it here. From large-scale markings of chinook fingerlings in the summer or fall of their first year, they obtained recoveries in the ocean fishery, the river fishery, and in the home streams. The ocean fisheries caught immature fish in their 3rd and 4th yr of life, and maturing fish in their 3rd, 4th, and 5th yr. The river fishery took nearly mature fish in their 3rd, 4th, and 5th yr.

The computations from these data are complex and will not be described here. No breakdown of the ocean catch by age was available, so it was impossible to estimate fishing and "natural" mortality rates separately. What was done was to estimate rates of fishing for a series of trial values

of total noncatch mortality (natural mortality plus the shaker losses of Sections 10–14), the same for all ages from 1+ onward.

55. Columbia River fall chinooks — A massive program of marking hatchery chinook fingerlings was carried out in 1961–64, and results have been reported in some detail by Cleaver (1969) and Henry (1971, 1972). Henry's papers include some data not available to Cleaver, and they modify some of the latter's tables by including partially regenerated mark combinations. Marking was by removing the adipose fin (Ad), the right or left maxillary bone (RM or LM), and sometimes one of the ventral fins as well (RV or LV). Neither Cleaver nor Henry had any objective estimate of noncatch mortality in the ocean, so they used a series of 6 trial rates from $M' = 0.02$ to 0.08 per mo, the same for ocean ages 1+, 2+, 3+, and 4+.

Tables 4 and 5 of Henry (1971) show the estimated rates of ocean fishing (F) on the 1962 and 1961 marked fish at ages 2+, 3+, and 4+, for each of the trial values of M′. Increase in M′ decreases estimates of F, but not very rapidly. There are some curious aspects of these two tables. For example, rate of fishing for the Spring Creek fish of the 1961 brood was more than twice that of the Kalama fish at age 2+, but only 20% as great at age 4+; this may reflect different distributions of the two stocks in the ocean. Another noteworthy fact is that at all ages the 1962 brood experienced a considerably larger ocean fishing rate than did the 1961 brood — about 50% larger on the average. It is impossible that the number of trollers could have increased this much in one year, but bad weather might have reduced catches, or different oceanographic conditions might change the distribution or behavior of the fish.

In Section 14 it was estimated that the shaker mortality for chinooks was equal to 1 fish killed for every 2 boated and landed. This means that the "natural" mortality rate in Cleaver's or Henry's tables should not be less than half of the weighted mean fishing mortality rate. This would eliminate 0.02 per mo as a possible value of M′ in most cases.

If we were to use some reasonable value for true natural mortality, say $M = 0.015$ per mo, and combine it with a shaker loss of $F/2$, it is possible to narrow the range of estimates of F. Thus values of F for $M' > 0.05$ per mo would be eliminated in most cases.

There is however, one important difficulty with the whole analysis: the natural mortality and, more importantly, the shaker loss both must bear more heavily on 3rd-yr fish than on older ones. New computations that take this into account would be desirable.

Inverse Weight Method

56. Procedure — The hypothesis that salmon natural mortality rates decrease with increase in size is supported by the fact that smaller sockeye smolts tend to have larger ocean mortality rates. This is apparent in three different types of comparisons. Within a year-class the average diameter of the freshwater zone of the scales, and the number of circuli in them, is greater among adult fish returning from the sea than it was among the smolts as they left the lake. Comparing different year-classes of a single stock, smolts of larger average size tend to survive better than the smaller ones, although this relationship is often weak relative to other causes of variation in survival. One of the best series is Table 1 of Foerster (1954), which gives data on smolt size and rate of return to Cultus Lake over 18 yr. Finally, stocks having larger smolts tend to have smaller marine mortality rates than those with small smolts; Ricker's (1962a) figure 1 indicates a negative curvilinear relation between instantaneous mortality rate and mean smolt length.

Young salmon when they enter the sea, particularly pinks and chums, are small enough to be eaten by a great number of predacious fishes, birds, and mammals. No direct estimates of the severity of these losses are available, but it is reasonable to imagine that most of the large mortality that occurs early in life is a result of predation or parasite attack. As they grow, young salmon of all species become potential prey for fewer and fewer predators. Less is known about parasites, but at least there are no macroscopic ones capable of killing large salmon. At a weight of about 250 g salmon are no longer available to most birds. On the high seas the only consistent large predators appear to be salmon sharks (*Lamna ditropis*) and fur seals. When later they move toward shore they leave these species behind and encounter blue sharks, sea lions and harbour seals, but since the two latter are much less abundant than the fur seals there is no reason to suppose the coastal region is any more dangerous than is the open sea. Another salmon predator is the lamprey (*Lampetra tridentatus*), but its distribution in salt water is little known. There are also reports of the consumption of good-sized salmon by halibut, and killer whales capture some, but the number of predators that can take a large salmon is very limited.

Considerations such as the above led S. B. Mathews to suggest that ocean mortality rate

might be an inverse function of the weight of the fish — an objective and intuitively reasonable hypothesis that would seem superior to the various assumptions used in Fredin's Models 1–4. Mathews applied the method to cohos, for which the procedure was to combine this hypothesis with a simple expression for rate of growth throughout ocean life (Section 57). However it can also be applied to situations where no simple mathematical formulation of growth is possible (Section 58).

57. Puget Sound cohos — S. B. Mathews[2] applied the inverse weight method to a stock of cohos that spends its marine life within Puget Sound. To data for the marine phase of their life he fitted a simple exponential curve:

$$w = ae^{bt} \qquad (15)$$

where w is weight in grams, and t is time in months from the time the smolts enter salt water at the beginning of May at a weight of 0.05 lb or 22.68 g. Final weight was taken as 5 lb or 2268 g 17 mo later. Inserting these values, (15) becomes:

$$w = 22.68e^{0.271t} \qquad (16)$$

Some observations at intermediate sizes agreed with (16) fairly well.

Mathews points out that if instantaneous natural mortality rate M_t is inversely proportional to weight, and k is a proportionality constant, then from (15):

$$M_t = \frac{k}{w_t} = \frac{k}{a}e^{-bt} = Ke^{-bt} \qquad (17)$$

Given a single estimate of M_t at any time during the life history, the constant K can be calculated, and hence the value of M_t at all stages of ocean life. Alternatively, knowing the overall natural survival rate S from smolt to adult, the instantaneous natural mortality rate is $-\log_e S = Z$; this is equal to the sum of the instantaneous mortalities throughout ocean life, so that K can be estimated from:

$$\int_{t=0}^{t=17} Ke^{-bt} = Z \qquad (18)$$

Survival rates of Puget Sound hatchery cohos marked by removing a maxillary bone and a ventral fin have been reported by Senn (1970a, b) and Senn and Satterthwaite (1971). A group of five hatcheries in the southern part of the Sound had consistently the largest survival rates, and hence should be closest to the performance of wild fish of comparable size. Observed returns are shown in table 10 of each of the papers cited, augmented by the factor 1.25 to adjust for the mark handicap. From the adjusted returns to fisheries and to the hatcheries, the instantaneous mortality rates below have been computed:

	Brood		
Kind of mortality	1964	1965	1966
1. Total	4.26	3.71	3.71
2. Noncatch	2.88	2.20	2.50
3. Catch (F)	1.38	1.51	1.21
4. Shaker loss (F/2)	0.69	0.76	0.60
5. Natural	2.19	1.44	1.90

The first two lines are the primary data, and F is obtained from them by subtraction. Shaker loss is estimated as half the catch (Section 14), and the natural mortality rate is the difference between lines 4 and 2.

The mean natural mortality rate is 1.84. Inserting this figure in expression (18) we obtain:

$$K\left[\frac{e^{-4.607}}{-0.271} - \frac{1}{-0.271}\right] = 1.84 \qquad (19)$$

and K = 0.504. This can now be inserted in (17) to compute monthly natural mortality rates on the 1st day of successive months. For the latter part of life these are as follows:

Month	M	Month	M
8 (Jan. 1)	0.058	13 (June 1)	0.015
9 (Feb. 1)	0.044	14 (July 1)	0.011
10 (Mar. 1)	0.034	15 (Aug. 1)	0.009
11 (Apr. 1)	0.026	16 (Sept. 1)	0.007
12 (May 1)	0.020	17 (Oct. 1)	0.005

The above refers to hatchery-reared fish of about 23 g when released. The total natural mortality experienced by these fish, averaging 1.84, is greater than the 1.44 maximum estimate for wild coho smolts in Section 27, in spite of the fact that the latter were smaller when released (14 g as compared with 23 g). This suggests that the hatchery smolts are less viable — even those from the best of the Puget Sound establishments.

58. Karluk sockeye — Figure 3 of Section 75 shows the ocean growth in weight of age 2/3 Karluk sockeye. Mean weights for each month were read off curve B of Fig. 3 and are entered in column 2 of Table 7. Their reciprocal (column 3) represents the relative share of the total mor-

[2]The procedure and information used here are from an unpublished manuscript "An exponential model for natural mortality rate of Pacific salmon," 10 p., 1974. The method is elaborated by Mathews and Buckley (1976), whose paper deals, however, with cohos that leave Puget Sound.

TABLE 7. Computation of monthly instantaneous mortality rates for a group of Karluk sockeye of the 2/3 life history type. Mortality rate is inversely proportional to the mean weight of the fish each month. Colums 2–4 use growth curve B of Fig. 3; columns 5–7 use curve A.

1 Month	2 Mean wt (*g*)	3 Relative mortality 100,000/wt	4 Mortality rate	5 Mean wt (*g*)	6 Relative mortality 100,000/wt	7 Mortality rate
June[a]	30	2222[a]	0.255[a]	27	2469[a]	0.237[a]
July	60	1667	0.192	50	2000	0.229
Aug.	90	1111	0.128	80	1250	0.143
Sept.	120	833	0.096	170	588	0.067
Oct.	160	625	0.072	230	435	0.050
Nov.	190	526	0.060	270	370	0.042
Dec.	230	435	0.050	300	333	0.038
Jan.	270	370	0.043	310	323	0.037
Feb.	310	323	0.037	320	312	0.036
Mar.	360	278	0.032	330	303	0.035
Apr.	420	238	0.027	350	286	0.033
May	470	213	0.024	390	256	0.029
June	520	192	0.022	450	222	0.025
July	580	172	0.020	560	179	0.020
Aug.	640	156	0.018	680	147	0.017
Sept.	710	141	0.016	830	120	0.014
Oct.	780	128	0.015	960	104	0.012
Nov.	850	118	0.014	1030	97	0.011
Dec.	940	106	0.012	1080	93	0.011
Jan.	1020	98	0.011	1120	89	0.010
Feb.	1120	89	0.010	1150	87	0.010
Mar.	1240	81	0.009	1210	83	0.010
Apr.	1360	74	0.009	1310	76	0.009
May	1510	66	0.008	1460	68	0.008
June[b]	1650	20[b]	0.002[b]	1620	31[b]	0.004[b]
Total		10282	1.182		10321	1.182

[a] ½ mo.
[b] ½ mo.

tality assigned to each month (the first and last periods are less than a month and are adjusted accordingly). These shares are used as weighting factors to divide up Fredin's (1964) estimate of the total ocean mortality of Karluk 2-freshwater sockeye by months, which was 0.413 per mo when adjusted (Section 26). The mean length of ocean life of the smolts was 28.63 mo, so their total mortality averaged 1.182. The age 2/3 sockeye spent only 24 mo in the ocean, on the average, but it is better to assign them the mean mortality rate 1.182 because they would suffer the same heavy mortality when small as did the 2/4 individuals. This mortality rate is applied to the separate months in column 4, proportionally to the weight reciprocals of column 3.

Curve A in Fig. 3 is drawn to show a seasonal distribution of growth similar to what is suggested for western Alaska sockeye in Lander and Tanonaka's (1964) figure 17. Mean weights from this curve are shown in column 5 of Table 7, column 6 shows their reciprocals, and column 7 the correspondingly monthly mortality rates. In column 7 mortality rates are greater during early sea life than in column 4, but they are practically the same during the last 6 mo.

The time of annulus formation used in Fig. 3 and Table 7 is March 1. This date is not known with any precision, and it may become later in the year with increasing age. However, moving it a month or so ahead or back makes little difference to the picture of mortality distribution.

COMPARISON OF MORTALITIES METHOD

59. Procedure — Instead of making the somewhat arbitrary assumption that mortality rate is inversely proportional to size throughout life, we can obtain a series of mortality rates for fish of different sizes from available data. In Fig. 2 are

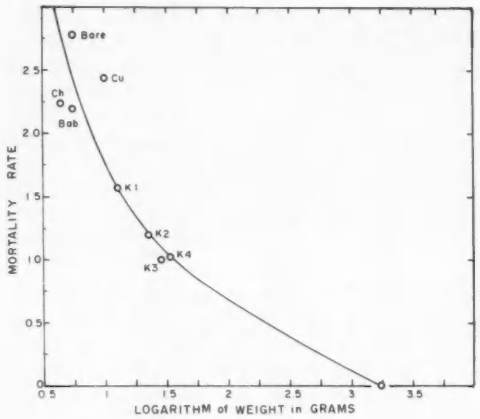

FIG. 2. Relation between total instantaneous mortality rate from smolt to adult and the base-10 logarithm of smolt size. The freehand fitted line is extended to an adult weight of 1.7 kg on the abscissa. Symbols identify the stocks (see the text).

plotted the observed total mortality rates of sockeye smolts, adjusted for mark handicap when necessary, for the whole of their ocean life (excluding fishing). It is similar to figure 1 of Ricker (1962a), but the logarithm of smolt weight is put on the abscissa instead of length, and the mark handicap factor of 1.37 is used. The line is fitted freehand among these points, and is brought down to an abscissal value equal to the logarithm of the mean weight of whatever group is under consideration. The line shown is for Karluk sockeye of age 2/3, having a mean adult weight of 1700 g (table B of Ricker 1962a).

60. Karluk sockeye — The comparison method is easiest to apply to species or stocks that mature mainly at one ocean age. However, we will attempt a more difficult case. The Karluk 2-freshwater sockeye growth curve A of Fig. 3 is used, which applies to the 2/3 life-history type. Columns 2 and 3 of Table 8 show weights from this curve, and their base-10 logarithms, at the start of successive months. Column 4 is the relative total mortality for each weight, read from Fig. 2. Column 5 is the difference between successive items in column 4, being a relative estimate of mortality rate each month. This could be adjusted to the observed total mortality for this group of fish by multiplying by 1.182/1.27 = 0.9307.

However there is a problem. In this computation the length of ocean life of 2-freshwater sockeye has been taken as 24 mo, to correspond with the growth curve of Fig. 3; that is, they have all been considered as age 2/3 at maturity. In fact, however, 2-freshwater sockeye mature in numbers after both 3 and 4 ocean growing seasons, the average length of time in salt water being 28.63 mo (Table 5). Thus the ocean mortality rate is spread over 4.63 mo more than are used in Table 8, which means, in turn, that monthly rates computed as in the last paragraph would be too large. We can adjust for this approximately by dividing all the rates by 24/28.63 = 0.8383. Combining this with the 0.9307 of the last paragraph gives a factor 0.7802 by which the column-5 figures should be multiplied. The resulting values are in column 6.[3]

The estimates of instantaneous mortality rates for older fish in Table 8 are not too different from those obtained by the inverse weight method, although somewhat larger. Considering May 1–September 1 as "summer", a comparison is as follows:

	Instantaneous mortality rate per mo	
	Inverse wt method	Comparison of mortalities method
Penultimate summer (4 mo)	0.022	0.033
Final winter (8 mo)	0.012	0.011
Final summer (1.3 mo)	0.008	0.030
Total for the above period	0.194	0.259
Total for final 12 mo	0.158	0.231

Actually the part of the line on Fig. 2 that is to the right of abscissal value 1.5 could well be drawn with more slope near the smolt sizes and less near the final weight, so that mortality estimates during the final year or so would be reduced.

SUMMARY OF NATURAL MORTALITIES

61. Sockeye — Table 9 summarizes the natural mortality estimates for sockeye. Those that represent averages for the whole of ocean life are reliable, but not of the greatest interest for growth–mortality comparisons. Some of the estimates that introduce arbitrary constants may be reasonable enough, but in effect they assume the quantities that we would like to estimate. Those

[3]Another way to make the computation would be to draw curves on both Fig. 2 and Fig. 3 for 4-ocean as well as 3-ocean fish, assign a somewhat larger total mortality rate to the 4-ocean group than the 3-ocean, and thus draw up mortality schedules for both types. However, the figures obtained for the last 12–18 mo of ocean life are very similar.

TABLE 8. Computation of ocean mortality rates for Karluk 3-ocean sockeye by the comparison of mortalities method. See explanation in the text.

1 Time	2 wt (*g*)	3 Log wt	4 "Mortality" to end of life	5 Difference	6 Mortality for month
June 10	20	1.30	1.29	0.21[a]	0.164[a]
July 1	30	1.48	1.08	0.25	0.195
Aug. 1	60	1.78	0.83	0.19	0.148
Sept. 1	120	2.08	0.64	0.14	0.109
Oct. 1	200	2.30	0.50	0.05	0.039
Nov. 1	250	2.40	0.45	0.03	0.023
Dec. 1	290	2.46	0.42	0.02	0.016
Jan. 1	300	2.48	0.40	0.01	0.008
Feb. 1	310	2.49	0.39	0.01	0.008
Mar. 1	330	2.52	0.38	0.01	0.008
Apr. 1	350	2.54	0.37	0.02	0.016
May 1	370	2.57	0.35	0.02	0.016
June 1	410	2.61	0.33	0.05	0.039
July 1	500	2.70	0.38	0.05	0.039
Aug. 1	610	2.79	0.23	0.05	0.039
Sept. 1	750	2.88	0.18	0.02	0.016
Oct. 1	910	2.96	0.14	0.02	0.016
Nov. 1	1000	3.00	0.12	0.01	0.008
Dec. 1	1060	3.03	0.11	0.01	0.008
Jan. 1	1100	3.04	0.10	0.00	0.000
Feb. 1	1130	3.05	0.10	0.01	0.008
Mar. 1	1170	3.07	0.09	0.02	0.016
Apr. 1	1260	3.10	0.07	0.02	0.016
May 1	1370	3.14	0.05	0.03	0.023
June 1	1570	3.20	0.02	0.02[b]	0.016[b]
June 10	1680	3.23			
Total				1.27	0.994

[a] $\frac{2}{3}$ mo.
[b] $\frac{1}{3}$ mo.

with a bias upward are of course maximum values, but as such they do not conflict with the unbiased estimates. Both the inverse weight and the mortality comparison method yield estimates for the entire ocean life (Tables 7 and 8), but for convenience Table 9 shows only the last year. The inverse weight method includes the assumption that mortality is inversely proportional to weight, which is reasonable but unproven.

Estimates for the last year of life that are without known bias and have small or moderate sampling errors are as follows:

Method	Natural mortality per mo
Comparison of life histories	0.014
Inverse weight	0.012
Mortality comparison	0.019
GM	0.015

In good agreement with the above are the estimate of 0.018 per mo for the penultimate 12 mo of ocean life by the ocean immatures method; and also the three estimates for the whole of pelagic (noncoastal) life by Parker's maturity schedule method, particularly the one with least sampling error (Karluk), which is 0.020 per mo.

62. Pinks, chums, cohos, and chinooks — Table 10 summarizes the estimates of natural mortality for these species. Most of them are upper limits, but the figures 0.019 and 0.017 are unlikely to be very much too large. A mean estimate of 0.013 per mo during the last year of life for cohos and chums is the best figure available from these data. The corresponding figure for pinks is probably somewhat larger, and that for chinooks somewhat smaller, because of the respective mean weights of these two species.

TABLE 9. Summary of estimates of the mean monthly instantaneous rate of ocean mortality for sockeye salmon. Items marked with an asterisk include a mark handicap ratio of 1.37, and in most cases have been reduced by 7% from the published figure which was based on a ratio of 1.27. Estimates with known bias are in a separate column, and the nature of the bias is indicated; "arbitrary" indicates that an arbitrary numerical value was used in computing the estimate. Numbers in the "Locality" column indicate the Section of this paper in which the computation is outlined.

Method	Author	Locality	Life history: Freshwater	Life history: Ocean	Ocean mortality period	Mean monthly mortality rate: Unbiased	Mean monthly mortality rate: Biased	Nature of bias, etc.	Sampling error
Smolt survival	Ricker 1962	Karluk (25)	1	—[a]	Whole ocean life	0.049*			Moderate
		" "	2	—[a]	" " "	0.042*			Small
		" "	3	—[a]	" " "	0.036*			"
		" "	4	—[a]	" " "	0.037*			Moderate
Smolt survival	Fredin 1964	Karluk (26)	1	—[a]	Whole ocean life	0.046*			Moderate
		" "	2	—[a]	" " "	0.041*			Small
		" "	3	—[a]	" " "	0.036*			"
		" "	4	—[a]	" " "	0.037*			Moderate
Maturity schedule (1)	Parker 1962	Karluk (29)	2+3	—[a]	All except "coastal" life	0.020*			Moderate
		Cultus (30)	1	—[a]	" " " "	0.039*			Very large
		Dalnee (31)	1+2	—[a]	" " " "		0.029*	Too large	Moderate
		Hook Nose (32)	1+2	—[a]	" " " "	0.030*			Very large
Mortality distribution	Fredin 1964	Karluk model 2 (35)	2	—[a]	Whole ocean life	0–0.060*		Arbitary	
		" " " "	3	—[a]	" " "	0–0.051*			
		" " 3 (36)	2	—[a]	After 1st 6 ocean mo	0.014*		"	
		" " " "	3	—[a]	" " " " "	0.012*		"	
		" " 4 (37)	2+3	—[a]	After 1st ocean mo	0.021*		"	Small
Comparison of life histories	This paper	Skeena (Babine) (40)	1	4	Last year of ocean life	0.014			Moderate
Smolt indices	Fredin 1965	Karluk (46)	2	4	Final 10.67 mo		0.029*	Too large	Large
	This paper	" "	2	4	" " "	0			Large
Maturity schedule (2)	Fredin 1965	Bristol Bay (42)	2	—[a]	12 mo preceding May 1 of final year		0.028	Too large	Unknown
	This paper	" " "	2	—[a]	12 mo preceding May 1 of final year	0.020		Arbitrary	Unknown
Dichotomy and maturity schedule	Mathews 1968	Bristol Bay (48)	1+2	4	Final 12 mo		0.049	Too large	Unknown
Taguchi's	Taguchi 1961c	West Kamchatka (53)	1+2	—[a]	Last 85 days		0.692	Too large	Unknown
Ocean immatures	Fredin 1965	Bristol Bay (44)	1+2	4	Penultimate 12 mo	0.018			Moderate
Inverse weight	This paper	Karluk (58)	2	3	Final 12 mo	0.012*			Small
Mortality comparison	This paper	Karluk (60)	2	3	Final 12 mo	0.019*			Moderate

[a]Includes all ocean types produced by the corresponding freshwater age.

TABLE 10. Summary of estimates of the mean monthly instantaneous rate of ocean mortality for salmon other than sockeye.

Species	Method	Author	Locality	Ocean mortality period	Mean monthly mortality rate: Unbiased	Mean monthly mortality rate: Biased	Nature of bias	Sampling error
Chinook	Ocean tagging	Parker 1960	Southeastern Alaska (21)	Mainly age 3–5		0.035[a]	Too large	Unknown, probably moderate
Coho	Limit mean	Lander and Henry 1973	Lower Columbia (50)	Last 12 mo		0.063[a]	Too large	Small
Coho	Double ocean tagging	Mathews and Buckley 1974	Puget Sound (23)	Early in last ocean year		0.185	Too large	Large
Coho	Inverse weight	Mathews and Buckley 1974, modified	Puget Sound (57)	Last 6 mo	0.013			Unknown
Coho	Smolt survival	This paper	Cultus Lake (27)	Whole ocean life		0.080	Somewhat too large	Unknown
Pink and chum	Maturity schedule	Parker 1962b	Central B.C. (33)	Oceanic life (excluding "coastal" mortality)		0.019	Too large	Moderate
Chum	Comparison of life histories	Parker 1962a	Central B.C. (39)	Last 2 yr	0.011–0.016[b]	0.017	Somewhat too large	Moderate
Chum	Taguchi's	Taugchi 1961b	Soviet coast (52)	Final 100 days		0.381	Too large	Very large

[a]Includes noncatch losses caused by fishing.
[b]These are the adjustments of Parker's estimate made in this paper.

C. Estimates of Rate of Growth

General Considerations

63. Age determination — The two methods most used to determine age of salmon are the length-frequency method, and scale reading. The more time-consuming otolith reading has occasionally been used, but salmon scales are usually easily interpretable except when they have become badly eroded during maturation. Length suffices to distinguish most "jacks" — fish that have 1 less ocean growing season than the first major one among mature chinooks, cohos, and sockeye. When salmon have been marked before leaving fresh water, their age can be determined by inspection of the mark — provided it has not been repeated in adjacent years or in neighboring localities.

64. Selective sampling — Salmon used for age determinations have been caught in various ways, some of which are selective. If so, different segments of the population are unequally represented, so that caution is needed in arguing from the sample to the stock as a whole. In particular, fish from the commercial fishery tend to be larger than average, particularly if it is a gillnet fishery, while those in the escapement tend to be smaller than average (Larkin and McDonald 1968; Todd and Larkin 1971).

65. Weight–length relationships — For sockeye salmon there are weight–length relationships by Ricker (1962a) for Cultus Lake smolts and adults, and by Parker (1963) for fish gillnetted off western Alaska by Lander and Tanonaka. In comparable units they are as follows:

$$\text{Ricker: } \log w = -1.954 + 2.958 \log l \qquad (20)$$

$$\text{Parker: } \log w = -2.3652 + 3.2666 \log l \qquad (21)$$

Here w is whole weight in grams, l is fork length in centimeters, and logarithms are to the base 10. Parker's formula gives larger weights than Ricker's, increasingly so among larger fish; for example, a 60-cm sockeye weighs 2830 g and 2020 g, respectively. Both formulae are based on mean weights and lengths of whole age-groups or life-history types, rather than individual fish. Ricker's covers a wider length range — from 7- to 72-cm as compared with 34 to 61 cm for Parker's — and has a correspondingly smaller sampling error for the slope (exponent); however, Parker's agrees better with the relationship for other species. Some part of the difference between (20) and (21) appears to be real, and may have one or more of several causes, among them: 1) greater stomach contents in the ocean-caught fish; 2) selection by the gillnets of fish having a larger girth at a given length, at one or both ends of their range of maximum effectiveness; 3) a real average difference in body form between Bristol Bay and Cultus sockeye.

LeBrasseur and Parker (1964) present a relationship between mean weight and mean length for pink salmon 5 to 49 cm long, and computed an exponent of 3.25. The full equation, estimated from their figure 8, is:

$$\log w = -2.30 + 3.25 \log l \qquad (22)$$

Ricker (1964) obtained a very similar estimate for British Columbia ocean-caught pinks of fingerling to subadult size:

$$\log w = -2.253 + 3.2 \log l \qquad (23)$$

Ricker's (1964) estimate for ocean chum salmon of the same wide range of sizes is similar to that for pinks:

$$\log w = -2.220 + 3.2 \log l \qquad (24)$$

Many weight–length relationships in the literature are for a limited range of sizes and will give obviously incorrect values if extrapolated over a longer range.

Tagged Salmon Method

66. Procedure — Salmon have been tagged on the high seas and recaptured later, so that their actual increase in length is known. Unfortunately the effects of tagging and of carrying the tag probably affect the fish's growth, but to what extent is not known. Also, it is unusual to obtain a really reliable length measurement from recaptured fish, so that large numbers of observations are not usually available.

67. Sockeye, pinks, and chums — Taguchi (1961a) used information from the tagging experiments of Hartt (1959) to compute the instantaneous rates of growth (K) for tagged salmon that were recaptured during the current year, and also for those taken a year later. Mean instantaneous rates of increase in length per day are shown in Taguchi's table 1. In Table 11 here they are converted to terms of weight on the basis that the weight–length exponent is 3.2. Less abundant Japanese data gave generally similar results. Taguchi concludes that "the value of K of mature salmon is larger than that of immature." This reflects the slow winter growth that is involved in the following-year recoveries, not an inherently smaller growth rate of the younger fish.

Columns 4 and 5 of Table 11 show the actual

TABLE 11. Rates of increase in weight estimated from recaptures of tagged fish, assuming the exponent in the weight–length relation is 3.2. Based on Taguchi's (1961a) table 1, from Hartt (1959).

1	2 Instantaneous rate of increase in wt	3	4 % increase in wt	5
	Per day ($\times 10^6$)	Per mo	4 mo	12 mo
Recaptured same year				
Chums offshore	4794	0.144	78	—
Chums coastal	4147	0.124	64	—
Sockeye	5046	0.151	83	—
Pinks	8016	0.240	162	—
Recaptured next year				
Chums offshore	1366	0.041	—	64
Chums coastal	2029	0.061	—	108
Sockeye	1792	0.054	—	91

increases in weight for a 4-mo growing season (matures) and for 12 mo (immatures). Both figures are less than the actual if the tag affects growth rate, and such an effect is likely to be more important for the immatures because of their smaller size (Koo 1959).

68. Sockeye south of the Aleutian Islands — Parker (1963) worked with more extensive tagging data by Hartt (1962). He used only fish that had been measured by trained observers, which meant that coastal recoveries were excluded. There were only six usable recaptures in the current year that had been at large more than 30 days, and those taken in less than 30 days gave extremely varied results (Parker's figure 2), so that the estimate of growth in the current season had a large sampling error. However the values obtained are reasonable if allowance is made for some retardation of growth from tagging. The instantaneous rate of increase in weight is estimated as 0.079 per mo in the final year.

OCEAN SAMPLING METHOD

69. Procedure — If comprehensive and representative samples of salmon in the ocean are available over a period of time, growth of the fish can be estimated directly from them. A variant that usually gives a somewhat longer time span is to compare the ocean-caught fish with fish caught commercially in coastal fisheries. In either case there is the problem of avoiding distortions due to selective sampling, and due to different movements of stocks of fish of different mean size. Another problem is that of comparing fish measured in different physical condition, e.g. alive, freshly dead, during rigor mortis, after the latter, and when thawed after being frozen (LeBrasseur and Parker 1964, p. 1103; Lander and Tanonaka 1964).

70. Bristol Bay sockeye — Lander and Tanonaka (1964) averaged the sizes of sockeye taken off western Alaska during successive 10-day periods from May 1 to August 28 over the years 1956–60. Gillnets of several meshes were used, which provided near-random selection, and adjustment was made for the difference in length between fresh and thawed fish. The summary of growth in their figures 16 and 17 shows that: 1) 2-ocean maturing sockeye are much larger than 2-ocean immatures; 2) rate of increase in weight is more rapid in summer (May–August) than the mean rate for the rest of the year; 3) in the final year growth continued without any decrease in absolute increment per unit time right up to the time the fish arrive in coastal waters. The instantaneous rate of increase in weight during May–August of their final year was 0.09 for 3-ocean fish and 0.13 for 4-ocean fish (Lander and Tanonaka's table 12).

As discussed in Section 72, there is reason to believe these figures are too low to represent true growth rate, possibly because the male fish (which are larger) tend to move to the coast earlier than the females. One indication of this is that the above growth rates for the 4 summer mo are little larger than those computed for the whole final year from scale annuli (Section 75).

71. Pink salmon — Ricker (1964, figure 1) shows the seasonal growth of pink salmon as estimated from scattered data reported by Birman

(1960). The increase in weight during the last 5 mo of life was from 0.39 to 1.44 kg, or by 270%, which is an instantaneous rate of 0.261 per mo. Growth rate was greatest in April, and slowed down slightly to the end of their ocean life early in August.

LeBrasseur and Parker (1964) sampled pinks from Fitzhugh Sound in central British Columbia and in adjacent ocean areas and compared the growth picture with other data. The summary line in their figure 7 indicates less seasonal variation in growth rate than other studies have, particularly Birman's data and some North American observations by F. Neave (shown in LeBrasseur and Parker's figure 9). However, they point out that the flatness of their curve depends heavily on a sample of 11 fish taken in the Gulf of Alaska in January, whose home stream or streams could be almost anywhere, so it is likely that the true seasonal growth pattern is more like that of Lander and Tanonaka's sockeye. Converted to weight, LeBrasseur and Parker's mean curve shows that the absolute gain per unit time decreases only slightly during the last month of life. The increase from mid-April to mid-August is from 35.0 to 51.9 cm, corresponding to 523–1879 g; this is an increase of 259%, or an instantaneous rate of 0.320 per mo. This is similar to the gain indicated for Asian pinks.

72. Chum salmon — LaLanne (1971) used samples of chum salmon taken in the North Pacific and Bering Sea to estimate growth in a manner similar to the sockeye study of Lander and Tanonaka (1964). The summary graph (his figure 5) shows much more rapid growth from June to September than during the rest of the year, particularly after the 2nd ocean growing season. As with sockeye and pinks, the fish continued to grow rapidly until they were well into the coastal area. LaLanne's table 7 summarizes his observations in terms of instantaneous rate of increase in fork length per 10 days. Multiplying by 3 converts these figures to a monthly basis, and multiplying by 3.2 converts them to weight (expression 24). This gives for maturing fish of the dominant 0/4 age-group an instantaneous rate of growth of 0.086 for American chums and 0.144 for Asian chums. Comparison of ocean catches with coastal catches gives larger growth rates in the final 1–3 mo of life, shown in LaLanne's table 10. The rates for 0/4 fish average 0.248 for American chums and 0.212 for Asian chums. The difference is striking, particularly for the American fish. The figures are probably distorted by different movements of different stocks of fish having different average sizes. One general trend is for males, which are larger, to approach the coast sooner than females, which would artificially decrease the growth rate estimated solely from ocean catches of maturing fish. For a best average figure the mean of the two estimates might be used: 0.167 for American 0/4 chums and 0.178 for Asian.

73. Coho salmon — From about April 1 to the end of September in its 3rd and final yr of life, an average coho grows from 0.6 to 2.5 kg approximately in Puget Sound and the Strait of Georgia, and from 0.8 to 4.0 kg in the open Pacific. Based on a 6-mo average season, the corresponding instantaneous growth rates are 0.24 per mo in inside waters and 0.27 outside.

Back-Calculation Method

74. Procedure — Growth from year to year is estimated by measuring the distance between annuli on scales, and applying an appropriate relationship between body length and scale radius. Length may then be converted to weight using a weight-length equation found by observation. One weakness of the method lies in knowing when exactly the annulus is laid down, and whether this represents an interruption of growth. Information on these questions is rather scanty, and different authors have reached rather different conclusions (Bilton and Ludwig 1966). It is clear that time of annulus formation varies between species, and it may also vary between stocks, geographically or otherwise. The other weakness is that this method gives no clue to the seasonal distribution of growth, which must be estimated from other sources.

75. Sockeye salmon — Ricker (1962a tables A–C) summarized the results of computations of growth of Cultus Lake sockeye by Foerster (1929), and of Karluk sockeye by Barnaby (1932). Foerster has also computed increments for marked Cultus sockeye taken in the 1932 and 1933 fisheries.

The circled points in Fig. 3 show the ocean weights of age 2/3 Karluk sockeye as computed from their scales, Barnaby's length data having been converted to weight by Ricker (1962a, table 8). These fish were taken on June 10 in the shore fishery. For the date at which they migrated to sea as smolts we use June 10, the mean date given for age 2/3 sockeye by Fredin (1964, tables 1 and 2). In curve B of Fig. 3 the observed points are joined by a smoothly ascending curve, which would correspond to a hypothesis that growth is not set back by the cold of winter. The date of annulus formation is estimated to be

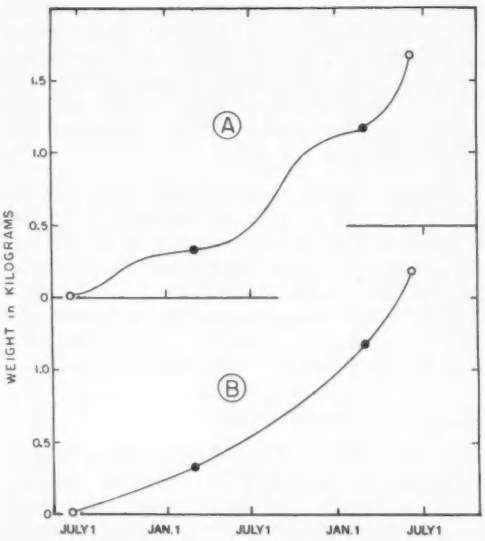

FIG. 3. Growth of Karluk sockeye of the 2/3 life history type, from smolt to adult. Black points are computed from scale annuli. Curve A is a possible seasonal distribution of weight increase, based on Lander and Tanonaka's (1964) observations. Curve B is a smooth curve joining the points, ignoring seasonal differences.

March 1. Curve A shows a possible seasonal growth curve based on the seasonal distribution indicated in figure 17 of Lander and Tanonaka (1964).

The instantaneous rates of increase in weight per month during the final growth year, calculated from these data, are shown below, together with values computed by Parker (1963, table 9):

		Growth rates	
Stock	Age	Here	Parker
Cultus	1/3	0.102	0.102
Karluk	2/3	0.156	0.154
Karluk	3/3	0.121	
Kuril	3-ocean		0.104[a]
Kuril	4-ocean		0.054[a]
Dalnee	3-ocean		0.093
Dalnee	4-ocean		0.065

[a]Mean of values for 1930 and 1944–50.

76. Pink salmon — Ricker (1964, tables 1–4, 9) summarized growth computations of pinks from four British Columbia and six Asian localities by various authors, as well as five collections made at sea. Weight increase from the annulus to coastal capture ranged from 190% to 590%, with only one sample less than 300%. Instantaneous rates were from 0.16 to 0.36 per mo, but most lay between 0.2 and 0.3.

77. Chum salmon — Ricker (1964, tables 5–8, 10) summarized growth computations of chums made by several authors from four North American and three Asian localities, as well as one collection from the high seas. Weight in the final growing season increased by 46–156%, the instantaneous rates being from 0.089 to 0.153 per mo. The younger maturing fish made much the largest *percentage* growth during their final year, but their absolute increase in size was sometimes less than that of older fish. In fact the absolute gain in weight made by 0/3, 0/4, and 0/5 fish in their final year was usually much the same.

In the case of Amur River autumn chums, Birman (1951) had samples taken at three successive ages from the 1943 year-class, shown below converted to weight using expression (24):

	Wt at annuli and when caught (*g*)				
Age	1	2	3	4	5
0/3	257	1534	2873		
0/4	211	1086	2449	3908	
0/5	203	950	1972	3451	5082

78. Chinook salmon — Parker and Larkin (1959, table 6) present back-calculated lengths of southeastern Alaska chinook salmon taken by trolling near Sitka. Except for the age 0/1+ individuals, a great majority of these would mature the same year; however, the length at capture is not given. Table 12 shows the same data transformed approximately to weight using expression (24) for chum salmon[4], which have a generally similar body form. The table illustrates that smaller fish tend to have somewhat larger rates of growth at all ages, but their absolute gains in weight are smaller.

METHOD OF COMPARING ADULT SIZES AT SUCCESSIVE AGES

79. Procedure — An approximate way to estimate growth rate is to compare the mean size of adults of particular sex and of two successive ages. For example, growth in the last year of life of 3-ocean sockeye would be estimated by comparing the mean size of mature fish having 2 and 3 ocean yr, respectively. However, there is a bias in all such estimates, because it has been found that the earlier-maturing salmon of a stock

[4]Parker and Kirkness (1956) give a weight–length relationship for chinooks of 63–108 cm fork length, but it is based on dressed weight. The exponent is 3.151.

TABLE 12. Calculated weights in grams of ocean-caught chinook salmon, computed from table 6 of Parker and Larkin (1959). Figures between the lines are the instantaneous rates of growth between the two weights immediately above.

Life history	Wt (*g*) at edge of annulus									
	1		2		3		4		5	
0/1+	248.4									
0/2+	134.6		1965							
		2.68								
0/3+	75.1		1496		4914					
		2.99		1.19						
0/4+	60.2		1110		3771		8857			
		2.91		1.22		0.85				
0/5+	20.5		705		2526		6275		13065	
		3.54		1.28		0.91		0.73		

TABLE 13. Mean weight in kilograms of maturing marked chinook salmon from two Columbia River hatcheries, and the instantaneous rates (G′) obtained by comparing the size of adjacent ages. Data were measured from fig. 9 of Henry (1972) and are the mean of the 1961 and 1962 year-classes.

	Kalama				Spring Creek				Overall mean
	Male		Female		Male		Female		
Age	Wt	G′	Wt	G′	Wt	G′	Wt	G′	G′
0/3	6.2		8.0		8.4		8.0		
		0.60		0.29		0.41		0.30	0.40
0/4	11.3		10.7		12.6		10.8		
		0.32		0.16		0.15		0.13	0.19
0/5	15.5		12.6		14.6		12.3		

always grow faster, on the average, than later-maturing ones. Thus, growth rates estimated by this method tend to be too small.

80. Sockeye salmon — Yamanaka (1963) apparently used the quotients of final year mean weights to estimate growth rates, although this is not entirely clear from his paper, as Parker (1963) has noted.

81. Chinook salmon — Henry (1972) observed the adult size of marked chinook salmon from the Kalama and Spring Brook hatcheries, taken in the Columbia River gillnet fishery. He compared the size of the maturing fish of ages 0/3, 0/4, and 0/5 to obtain their "apparent growth patterns." These were useful for comparative purposes; for example, the Kalama chinooks grew more slowly and had a greater mean age at maturity than the Spring Creek chinooks. The actual weights for the two year-classes with best age representation are summarized in Table 13. Mean instantaneous rates obtained by comparing adult sizes are 0.40 from age 3 to age 4 and 0.19 from age 4 to age 5. These may be compared with corresponding figures for Alaska chinooks from Table 12, which are $\log_e(8857/4914) = 0.59$ and $\log_e(13065/8857) = 0.39$ respectively.[5] However, the actual growth rates of the Alaska chinooks are greater than this by 0.26 and 0.34, respectively, and there is no question that a similar difference must occur on the Columbia. Consequently the instantaneous rates of Table 13 should be increased, probably by 0.3 or 0.4, if they are to be used as estimates of growth rate for the purpose of balancing mortality against growth, or in production computations. Similarly Henry's (1972) Bertalanffy growth curve would have to be modified.

SUMMARY

82. Growth by species and region — Table 14 is an attempt at an overall comparison of growth rates. It is based on the discussion in earlier Sec-

[5]The Alaska figures are not exactly comparable to those for the Columbia because they pertain to the penultimate year of life of fish that would mature one year later than the years quoted.

TABLE 14. Average instantaneous rate of growth per month during part or all of the final growing season for dominant life history types of five species of salmon. (Figures for chinooks are means for the penultimate growing season and are averages for a full 12 mo.) The species are arranged in order of increasing weight (kilograms) and of increasing number of growing seasons (including parts of seasons) typically spent in the ocean.

Species	Mean wt	Ocean seasons	Method		
			Tagging	Ocean sampling	Scale reading
Pink	2	2	0.23	0.29	0.26
Coho	4	2	—	0.27	—
Sockeye	3	3–4	0.11	(0.11)	0.12
Chum	5	4	0.12	0.17	0.12
Chinook					
Age 2–3	5	3	—	—	0.10
Age 3–4	9	4	—	—	0.07
Age 4–5	13	5	—	—	0.06

tions and on summaries for individual stocks or regions, as follows: for pink salmon by LeBrasseur and Parker (1964, table 17) and Ricker (1964, table 9); for sockeye by Parker (1963, table 9); and for chums by Ricker (1964, table 10).

We expect the results of the ocean sampling to give the largest values because they have been done during the season of rapid growth; however, the figure for sockeye is probably low for reasons discussed in Section 70. The tagging method also refers to the summer season, but the tag tends to slow growth somewhat. Estimates from scale reading refer to a longer period, including early spring months of slower growth, so give values smaller than the ocean sampling method. In the case of the chinooks the rates shown are for the last full year between successive annuli, so the figures are smaller than an estimate for the final growing season would be.

There is some indication that growth in the Bering Sea and the region off Kamchatka and the northern Kuril Islands is slower than in the Gulf of Alaska.

D. Comparisons of Yield With and Without Ocean Fishing

GAIN IN YIELD FROM FISH NOW BEING CAUGHT OR DESTROYED BY OCEAN GEAR

83. Balancing positive and negative factors — To calculate the loss from maintaining any high-seas fishery or the gain from discontinuing one, it is necessary to balance three effects: 1) Immediate or delayed mortality caused by fishing and not represented in catch statistics. 2) Increase in weight of the fish from the time of high-seas fishing to the time of the coastal fishery. 3) Natural mortality from the time of high-seas fishing to the time of the coastal fishery.

In all cases we assume that a coastal fishery exists or can be mounted that will capture all the salmon in excess of those required for spawning.

The magnitude of each of the above factors will vary with each fishery and each stock of fish. General guidelines as to what to expect are given for noncatch losses in Section 14, for growth in Table 14, and for natural mortality in Tables 9 and 10. Comparison of these figures shows that an ocean fishery will always take a smaller weight of catch than a coastal fishery that captures the survivors of the same fish when the ocean fishery is discontinued. The difference becomes greater, the earlier in the fish's life the ocean fishery is conducted. Superimposed on this is noncatch damage done to the fish by the gear, which is especially important when small nonmaturing salmon are being taken. Speaking generally, previous workers have mostly had adequate estimates of rate of growth, although a few have underestimated it. Estimates of natural mortality rate have usually been too large, often much too large. Losses caused by fishing gear have usually been ignored, or at any rate not used explicitly, by North American scientists who have compared growth and mortality, while those who estimated gear loss did not combine it with the growth and mortality picture. In Japan, on the other hand, Kisaburo Taguchi and Takeyuki Doi both made ingenious attempts to include all the factors in one formulation, but unfortunately the deficiencies of their data led them to wrong conclusions.

TABLE 15. Balance of growth and mortality in the high seas sockeye fishery, as computed by Parker (1963) (table 11).

1 Life history type	2 Time (*mo*)	3 Monthly instantaneous rate of change: Growth	4 Monthly instantaneous rate of change: Mortality	5 Monthly instantaneous rate of change: Mass	6 Total rate of change	7 Weighting factor
2+ ocean						
Final year	8	0.111	0.035	0.076	0.076	410
3+ ocean						
Penultimate year	8	0.059	0.026	0.033	0.264	143
Final year	4	0.075	0.026	0.049	0.196	446
Last month of final year	1	0.075	0.035	0.040	0.040	

Rather than attempt a series of new analyses for specific stocks, the Sections to follow consist mainly of brief comments on previous estimates, with approximate revisions where feasible.

84. Sockeye salmon — Taguchi (1961c) calculated that harvesting sockeye at sea increased the total yield because of an enormous natural mortality (0.69 per mo) during their last 2 mo of life. However there is no valid evidence for mortality on such a scale, and if any reasonable figure is used his equations indicate a considerable net loss from ocean fishing (Section 53).

For Cultus and Karluk sockeye Ricker (1962a) computed the effect of ocean fishing on yield, in terms of the gain in weight expected if the ocean catch were discontinued and the survivors of the fish that would have been taken pelagically were taken inshore instead. Computed gains were 100–182% for fish saved from capture at the start of their penultimate year. For fish taken during their final year the gain would be 7–13% for each month remaining before they reached the coast. These figures are a little too small because Ricker used too small an estimate of the marking handicap. Much more important is the fact that he had no estimate of noncatch losses. According to the figures given in Section 14 this would double the estimated gain from immatures, and would increase the gain from maturing fish by a third.

Parker (1963, table 11) balanced his estimates of growth rate and natural mortality rate for sockeye as shown in Table 15. The time periods chosen are those that elapse between high-seas fishing and the coastal fishery. The net changes shown in column 5 are positive in all cases, so that there is a gain in yield from harvesting fish near shore rather than on the high seas. Parker uses a basic natural mortality rate of 0.026 per mo for all months except the last, when it is 0.035. Growth rates are averages from several studies. Column 7 of Table 15 is an estimate of the relative weights of the ocean catch of 1957–59 that belonged to three classes: immatures (14.3%), maturing in the 3rd ocean yr (41.0%) and maturing in the 4th ocean yr (44.6%).

Parker's equation for the yield from harvesting these fish near shore is:

$$0.410e^{0.076} + 0.446e^{0.040} + 0.143e^{0.264+0.196+0.040} = 1.142$$

Hence the increase in yield is 14%, from the sockeye formerly caught on the high seas.

Taking all present information into account, we may adjust approximately for the principal defects of this estimate, by using a natural mortality rate of 0.02 per mo in the penultimate year and 0.015 in the final year, and allowing a noncatch mortality that is equal to the catch for immatures and equal to 25% of the catch for maturing fish (Section 14). This gives the expression:

$$1.333(0.410e^{0.060} + 0.446e^{0.060}) + 2 \times 0.143e^{0.312+0.240+0.060} = 1.76$$

Thus, the more realistic computation indicates a 76% gain from transferring the oceanic fishery to coastal waters. Actually this refers best to Alaskan sockeye, where the maturing fish are caught on the high seas about 1 mo (20–30 days) before they reach the coast. Using the approximately 2-mo period suggested by Taguchi (1961c) for Asian sockeye the equation becomes:

$$1.333(0.410e^{0.102} + 0.446e^{0.120}) + 2 \times 0.143e^{0.312+0.240+0.060} = 1.86$$

Fredin (1964, table 21) calculated the difference between growth and mortality for successive ocean years of 2- and 3-freshwater Karluk sockeye, using each of his four population models (Sections 26 and 35–37 here). These indicate a gain in bulk in all cases except for the last ocean

year of the unrealistic Model 1. As with Ricker's and Parker's estimates, the gain shown are all much too low because there is no allowance for noncatch mortality resulting from fishing.

Lander (1973) has stated that the biomass computations of Ricker (1962a, 1964), Parker (1963) and Fredin (1964) overestimate minimum losses of yield from high-seas fishing because they assume full availability of the stock on the high seas. Actually all three authors were estimating only the loss *from whatever fraction of a stock was taken on the high seas*, so that ocean availability does not come into consideration. They do assume (as does Lander) that shore and freshwater fisheries are able to harvest all the fish available that are in excess of breeding requirements.

85. Pink salmon — Doi (1962c) compared the total catches taken by fishing immature pink salmon at various rates and by fishing only mature ones. He calculated that total catch is increased by taking immatures when rate of fishing is small, but not when it is large. However, he used a very large rate of natural mortality, M = 1 per yr or 0.083 per mo, so that his results are not at all realistic. With natural mortality 0.02 or less per mo there is a large gain from using coastal rather than high-seas harvesting for all rates of fishing.

Ricker (1964, tables 11, 12) computed the losses from any pelagic harvesting of Bering Sea and British Columbia pink salmon, using a "likely" estimate of natural mortality (0.02 per mo and an "extreme" one (0.04 per mo and 0.07 in the last month). Using the "likely" estimates, Ricker's percentage losses can be converted to show the gains in yield from refraining from high-seas fishing, as follows:

Date of discontinued fishery	Percentage increase in catch: Bering Sea (%)	Percentage increase in catch: British Columbia (%)
Apr. 1	120	270
May 1	49	163
June 1	18	59
July 1	3	23
Aug. 1	—	5

Allowance for noncatch losses would increase all these figures by about 1/3 (Section 14).

86. Chum salmon — Taguchi (1961b) concluded that catching chums on the high seas increased the total yield from the stock. However, as with sockeye, the value for natural mortality used was so impossibly large that his estimates must be rejected (Section 52).

Ricker (1964, table 13) computed the losses from catching chum salmon at various times during their penultimate and final years. Converting these to gains from discontinuing ocean fishing, and using his "likely" natural mortality rate of 0.02 per mo, the increase in catch is 156% if fishing had been done on May 1 of the penultimate year, 52% if it had been done on May 1 of the final year, and smaller amounts for later dates. Allowance for noncatch losses increases these gains to 312% for the immature fish and to 69% for the maturing fish (Section 14). A natural mortality rate not greater than 0.015 now appears even more likely, so the above gains are still somewhat too small.

Gain in Total Yield from Discontinuing Ocean Fishing on the Scale that Now Exists

87. Procedure — All the above estimates indicate the gain that would be realized by discontinuing ocean fishing, in terms of a unit of catch now being taken on the high seas. It can also be asked, what is the effect, on total yield, of the high seas fishing as it is actually carried on? Ricker (1964) gave a general formula for calculating the loss from a fishery that takes H tons on the high seas (called the "ocean" catch below) at a particular time, and C tons at the coast. This can be expanded to take care of noncatch losses, given that the ocean catch plus the losses are equal to n times the ocean catch, i.e. nH. Let k be the difference between growth rate and natural mortality rate from the time of the ocean fishery to the time of the coastal fishery. The various possible comparisons are as follows:

Present total catch	$H + C$	(20)
Catch if ocean fishing stops	$nHe^k + C$	(21)
Difference	$H(ne^k - 1)$	(22)
Gain from stopping ocean fishing, as a fraction of the present catch	$\frac{H(ne^k - 1)}{H + C}$	(23)
Loss from ocean fishing, as a fraction of the possible catch	$\frac{H(ne^k - 1)}{nHe^k + C}$	(24)
Ratio of catches without and with ocean fishing	$\frac{nHe^k + C}{H + C}$	(25)

If the ocean fishery extends over a considerable period of time, the catch and the computation can be broken down into time segments and summed. Similarly if both mature and immature

TABLE 16. Observed ocean and river catch from unmarked fingerlings produced by two hatcheries, in metric tons, and the computed catch if all fishing were done in the river, for two different estimates of ocean natural mortality (M = 0.0375 and M = 0.02 per mo). K = Kalama Hatchery, SC = Spring Creek Hatchery. The year shown is the year of liberation of the fingerlings. (Cleaver [1969], tables 37 and 38 and Henry [1971], tables 10 and 11.)

	2	3	4	5	6	7
	M = 0.0375			M = 0.02		
1	K 1961	SC 1961	K 1962	K 1961	SC 1961	K 1962
Ocean catch	94	279	92	—	—	—
River catch	77	272	32	—	—	—
Total catch	171	551	124	171	551	124
Catch if all taken in the river	212	703	165	294	899	245
Difference	41	152	41	123	348	121
Increase in yield if all fishing were in the river	24%	28%	33%	72%	63%	98%

fish are taken, the loss from each should be calculated separately.

Three examples of computations of potential overall increases in yield, in fisheries importantly affected by ocean fishing, are given in the following Sections.

88. Pink salmon — As an example of the application of the expressions above, consider the 1970 catch of pink salmon in Asian waters. The oceanic catch was H = 31,200 tons and the catch by coastal fisheries was C = 21,500 tons. The ocean catch was taken mostly in June, about 2 mo before the average date of the Japanese and Soviet coastal fisheries. The rate of growth of pinks during this time is about 0.29 per mo (Table 14), and their mortality is about 0.015 per mo (Table 10). The difference is 0.275, so $k = 2 \times 0.275 = 0.55$. Finally, noncatch mortality in ocean fishing is estimated as 25%, hence $n = 1.333$. From expressions (20)–(25) we obtain:

Present catch	52,700 tons
Catch with no ocean fishing	93,600 tons
Difference	40,900 tons
Gain from discontinuing ocean fishing, as percentage of the present catch	78%
Loss due to ocean fishing, as percentage of the possible catch	44%
Ratio of catches	1.78

As mentioned before, the above assumes that the coastal fishery would capture the survivors of the fish no longer caught by the ocean fishery. A more exact computation would break the catches down by months, say, but since the coastal fisheries vary in time, and the contributions of each region to the ocean fisheries cannot be sorted out, it is not likely that much greater accuracy would be achieved.

89. Sockeye salmon — In Section 84 Parker's computation of losses from ocean fishing for Asian sockeye during 1957–59 was modified to indicate an 86% increase in yield from discontinuing that fishery. For west Kamchatka in 1957–59 Taguchi (1961c) quotes mean figures of 2000 tons taken at the coast and about 9900 tons on the high seas (6.6 million fish at an estimated 1.5 kg each). Then an 86% increase from abandoning ocean fishing would increase the *total* catch to:

$$(1.86 \times 9900 + 2000)/(9900 + 2000) = 1.72$$

times the actual total catch. The overall gain in yield is 72%.

90. Chinook salmon — Cleaver (1969) and Henry (1971) both calculated the increase in weight of fall chinook salmon entering the Columbia River if ocean fishing were to be abolished. They both used M = 0.0375 per mo and assumed that it was all natural mortality. The estimated gains in yield were from 24 to 33% (columns 2–4 of Table 16). However, much of this 0.0375 represents shaker loss that would be eliminated if ocean fishing were discontinued. Columns 5–7 of Table 16 are approximate computations from Henry's tables, assuming a true natural mortality of 0.02 per mo; these indicate yield increases of 63–98% from abandoning ocean fishing. However a completely new analysis would be desirable (see Section 55). A computation using expressions (20)–(25) would require a breakdown of the ocean catch by ocean age groups, which is not available.

Henry (1972, figure 12) calculated maximum potential yields for three broods of hatchery chinooks and compared them with present yields, for several natural mortality rates. For the smallest natural mortality rate that was used (M = 0.02 per mo) the actual yields were 70–75% of the potential. However Henry's potential yields are much too low, partly because growth rate is underestimated (it is from comparisons of the size of maturing fish), and partly because he fails to allow for any gain from eliminating shaker losses. In addition, a natural mortality rate of 0.02 is probably somewhat too large for the older fish.

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Production of Wild, Domestic, and Interstrain Hybrids of Brook Trout (*Salvelinus fontinalis*) in Natural Ponds

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FLICK, W. A., AND D. A. WEBSTER. 1976. Production of wild, domestic, and interstrain hybrids of brook trout (*Salvelinus fontinalis*) in natural ponds. J. Fish. Res. Board Can. 33: 1525–1539.

Hatchery-reared wild and domestic strains of brook trout (*Salvelinus fontinalis*) were released in natural lakes, and survival and growth estimated at semiannual intervals throughout the life span. Angling was restricted. Four experiments with two year-classes involved three different Adirondack Mountain (New York) wild strains and two domestic strains, a fifth experiment included two wild strains from James Bay, Quebec and a hybrid between one of these (Assinica Lake) and a New York domestic strain. Wild and hybrid strains consistently exhibited greater longevity (5–7 yr) compared with domestic (few recovered after 3 yr). Climax sizes were not much different, except the Domestic × Assinica hybrid that was substantially larger than either of the two parents. Gross production and yield to angling of any given strain cohort was correlated ($r = 0.93$) and life-span gross production was 50% greater for wild and hybrid groups per unit fish stocked. Biomass stocked per recruit was much larger for domestic strains, and taking this into account, the ratio of gross production to weight stocked was about 6 times greater. Increased costs of rearing nondomesticated strains, if any, must be taken into consideration in an economic evaluation, but use of wild and/or hybrid strains of trout offers significant benefits under management conditions of these experiments.

FLICK, W. A., AND D. A. WEBSTER. 1976. Production of wild, domestic, and interstrain hybrids of brook trout (*Salvelinus fontinalis*) in natural ponds. J. Fish. Res. Board Can. 33: 1525–1539.

Des lignées sauvages et domestiques d'ombles de fontaine (*Salvelinus fontinalis*) élevées en pisciculture ont été relâchées dans des lacs naturels. Leur survie et leur croissance ont ensuite été observées à intervalles semi-annuels durant toute leur vie. On a de plus limité la pêche à la ligne. Quatre expériences avec deux classes annuelles impliquèrent trois lignées sauvages et deux lignées domestiques différentes de la région des Adirondacks (New York); une cinquième expérience porta sur deux lignées sauvages de la baie James, Québec, et sur un hybride entre une de ces dernières (lac Assinica) et une lignée domestique new-yorkaise. Les lignées sauvages et hybrides montrent uniformément une longévité nettement plus grande (5–7 a.) que celle des lignées domestiques (peu ont été récupérées après 3 a.). Les tailles au stade de climax ne diffèrent pas de façon substantielle entre les nombreuses lignées sauvages et domestiques comparées, à l'exception de l'hybride domestique × Assinica, nettement plus grand que l'un ou l'autre des deux parents. Nous avons établi la corrélation ($r = 0.93$) entre la production brute et le rendement de pêche à la ligne d'une cohorte de lignée donnée et observé que la production brute était 50% plus grande pour les groupes sauvages et hybrides par unité de peuplement. La biomasse du peuplement par recrue est beaucoup plus élevée pour les lignées domestiques et, en tenant compte de ce fait, le rapport production brute/poids de peuplement est à peu près 6 fois plus grand. On doit prendre en considération, s'il y a lieu, les coûts plus élevés d'élevage de lignées non domestiques, mais l'emploi de lignées sauvages et/ou hybrides d'ombles de fontaine offre des avantages économiques marqués dans les conditions de gestion de ces expériences.

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SURVIVAL under natural conditions is often deficient in inbred hatchery strains of certain salmonids. Where longevity is important, high mortality in stocked fish limits management options and increased cost. The life-span production of several year-classes of brook trout (*Salvelinus fontinalis*) of varying wild and domestic parentage is covered in this contribution, and the data are examined in terms of relative management potential. Earlier related studies have reported on this as well as other comparative attributes of

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wild and domestic strains of brook trout (Vincent 1960; Hatch and Webster 1961; Flick and Webster 1964; Green 1964; Moyle 1966).

The procedure followed in these experiments has been to rear various strains of brook trout under similar hatchery conditions and to release them in a common body of water, where growth and survival could be assured through the life span of each year-class. Parameters of vital statistics have then been computed to provide a basis for comparing production in wild, domestic, and interstrain hybrid strains. Data are also appropriate for intensive study of population dynamics and management of brook trout in lakes and ponds, to be considered in a later contribution.

The five experiments are part of a series designed to yield information on various management schemes for brook trout, especially under pond conditions. Two of the experiments involved successive year-classes, 1959 and 1960, of the same two wild and one domestic strain that were released initially in two different ponds, Bear and Long. Circumstances required reclamation of Bear Pond in the year following release of the 1959 year-class, so that a maximum of trapped survivors was transferred to Long Pond for the completion of the experiment with this year-class. An additional two experiments were conducted with two strains of the 1961 year-class, involving the same two ponds, but with one of the plantings made initially in a small drainable pond and transferred to Long Pond in the spring of the 2nd yr. The fifth experiment evaluated an interstrain hybrid between a wild Canadian and a New York domestic strain.

A constraint in these experiments has been the necessity to restrict the number of fish initially stocked so that greatly reduced growth rates did not develop from overcrowding and yet still allow sufficient numbers of fish in each group to survive through the life span. This necessitated restrictions on angling mortality, a control greatly enhanced by conducting the investigations on private waters. Even so, numbers of fish surviving into the 4th and 5th yr were barely minimal to provide a basis for the calculations required. However, the main comparative statistics were well established by data obtained prior to attainment of senescent ages.

Materials and Methods

Strains of Trout

Domestic — Two strains were involved, both described earlier by Vincent (1960) and Flick and Webster (1964), and are those referred to as the "Berlin" strain propagated by the U.S. Fish and Wildlife Service in the eastern United States, and the "New York" strain. Either by intent, or inadvertently, both have been maintained as inbred lines for some 50 or more yr. They are characterized by early maturity (most males at age 0+), robustness of form, and good hatchery growth. The two groups appear to exhibit similar performance after planting, and no distinction will be made between them in this paper.

Wild — Moyle (1966) discussed the ambiguity of the term "wild" as used in current literature. He suggested that the term "F_1 wild" to be used for the first generation of hatchery-reared fish from parents that hatched and matured under natural conditions in a native environment. Parental stocks would be distinguished by designation as "wild" fish. Within this framework, the groups of wild trout involved experimentally in these tests are F_1 wild. Native brook trout from three Adirondack watersheds and from two Quebec river systems were involved: Honnedaga Lake, in the southwestern Adirondacks, exhibits unusual chemical and physical characteristics, of which low pH and unusually high heavy metals concentration are noteworthy (Schofield 1965). Brook trout is the only fish species still extant, reaching 1–1½ kg in weight at ages 7–8 yr (Webster 1961). Horn Lake is a relatively inaccessible mountain-top pond in the Black River system, under private control for about 75 yr. Long Pond Outlet is a small stream typical of many small low gradient upland waterways containing a population of small stunted trout (Flick and Webster 1975). This stream, in the St. Regis–St. Lawrence watershed, forms the outlet of one of the study ponds and lies within a few miles of the other test waters.

The Canadian strains came from the Rupert and the Broadback River systems discharging into the southeast corner of James Bay. These adjacent systems contain numerous lakes and rivers; eggs were obtained from trout captured in the vicinity of two of them, the Temiscamie River and Assinica Lake. Both stocks of trout reach a large size, commonly 2 kg or more, with occasional fish in the Broadback system (Assinica Lake) reaching 5 kg, but they differ in other respects. Longevity in Assinica trout appears to be about 9 yr, an age confirmed by individual fish naturalized in one Adirondack water. Assinica trout are late maturing (ages 2–4), compared with Temiscamie (ages 1–3); the latter are more brilliantly colored as both juveniles and adults, especially in the intensity of the spotting. Phenotypic differences in color pattern persisted in populations stocked concurrently in the same Adirondack waters. The relationships of these stocks to the river–lake complex and details of life history are unknown.

Initial introductions of Assinica and Temiscamie strains were made with the 1962 and 1967 year-classes, respectively, from eggs provided by the Department of Tourism, Province of Quebec. The number of parents involved in each instance was small, some 10–20 individuals.

TABLE 1. Descriptive statistics of Brandon and Bay Pond Park ponds used for comparative studies of survival of domestic and wild strains of brook trout (*Salvelinus fontinalis*).

Name of pond	Area (*ha*)	Depth (*m*)		Transparency (*Secchi*) *m*	Thermally stratified	Oxygen deficit	Color
		Max	Avg				
Laramie	0.19	1.5	~.6	—	—	No	Clear
Bear	18.6	5.8	4.6	4.0	Yes	Yes	Green
Long	17.8	3.0	1.7	1.5	Weak	Yes	Dark brown
Bay	87.0	20.2	5.2	2.4	Yes	Yes	Brown

Hybrid — Crosses between the Canadian and domestic strains were made using the latter as the maternal parent (initially because of a limited number of eggs of the wild stocks). Only the Assinica hybrid data are presented in this paper.

TEST WATERS

Test ponds are located on private lands known as Brandon and Bay Pond parks located on the headwaters of the middle and west branches of the St. Regis River in the northern Adirondack Mountains of New York State (towns of Waverly and Santa Clara, Franklin County, at approximately long. 74°25′, lat. 44°23′). All waters are natural basins lying in areas of kame topography at elevations of about 470 m. While classified as mesotrophic to somewhat dystrophic in character, as a group they are relatively infertile. Bear Pond is an unusually productive exception and has been subject to winterkill in recent years of prolonged and heavy snow cover. Lethal conditions were averted by deep pumping in late winter during those years when critical oxygen deficits appeared likely to develop (Flick 1968). Four experiments were initiated in waters devoid of fish life, either the result of drainage (Laramie Pond), winterkill (Bear Pond in 1958–59), or reclamation with rotenone (Long and Bear Ponds 1960; Bay Pond 1968). The 1960 year-class in Long Pond was released following an earlier transfer of 46 age 0+ and 473 age 1+ and older trout, forming a standing crop of about 6.7 kg/ha (6 lb/acre). Natural reproduction quickly saturated all waters in the 2nd and 3rd yr of the experiments. Characteristics of the several waters are given in Table 1.

Bay Pond was the only water with a forage fish species. Alewives (*Alosa pseudoharengus*) were introduced as adults in the spring of 1969 and spawning during that and subsequent years presumably influenced trout growth.

Barrier dams were present on the outlets of all ponds. Barrier screens or downstream-inclined screen-type traps operated as effective deterrents to in-migration although in some instances were not always functional during heavy spring runoff periods in Long and Bay ponds. In Laramie and Bear ponds, outlet streams were small and the barrier screens and/or traps were easily maintained.

ANGLING

Angling was closely controlled. On Brandon Park, all fish were checked by trained observers, while on Bay Pond Park most fish were processed by individual anglers at a central station. Only a few people were involved so that instruction regarding data to be collected was believed effective in providing reliable and complete information on the catch in Bay Pond.

Creel limits were usually 10 fish (5 in Bay Pond) and size of fish retained was largely determined by the climax size prevailing in each individual water. Except for limited use of worms in Bay Pond, angling was restricted to artificial lures and fly fishing predominated. This regulation permitted the release of substantial numbers of fish without serious injury. Although formal quotas were not established on numbers of fish to be removed, total fish killed was restricted on an ad hoc basis. Fishing time of each angler was recorded to the nearest ½ h, and data collected on length, weight, sex, and mark. Most of the angling catch occurred in spring.

HATCHERY AND PLANTING PROCEDURES

Trout used were reared at several different fish culture facilities. Stresses due to the hatchery environment undoubtedly varied, especially for the wild strains. Experiments involving paired or multiple plantings in a single water used groups reared at the same station and hence subjected to as uniform conditions and care as possible. However, inherent differences in wild and domestic strains on such important factors as wildness, nutritional adaptation to artificial diets, and disease resistance are presumed to have played a role in shaping the end product available for testing. In all instances, factors such as these would seem to favor domestic stocks within a hatchery environment. We believe this is so because invariably domestic groups were substantially larger at planting and generally experienced less mortality in the hatchery. Details on the several plantings are entered in the headings and top line of Table 3–5, referred to subsequently.

The extent to which differential hatchery mortality may have affected the gene pool of the several groups involved here is unknown and the problem is complicated by differential mortality at various stages

in development. Tyler (1964) found that mortality from egg to 18-wk-old fingerlings was 50% for a domestic strain and 32–33% for two wild groups (same strains as in 1959–60 year-classes reported here). However, most of the mortality in the domestic group was pre-eyed and regarded as usual in this domestic stock. Improved cultural techniques, such as automated feeding and high fat diet, have greatly improved hatchery performance of wild strains. For example, the 1969 year-class evaluated in this paper experienced hatchery mortalities from the feeding fry to fall fingerlings of 18, 29, and 11% in Temiscamie, Assinica, and hybrid strains, hence comparable with domestic strains (I. Annis personal communication).

Experiments were initiated by plantings of spring or fall fingerlings, where each strain cohort was identified by an excised fin removed just prior to release. There was no evidence of excessive mortality associated with finclipping as presumed by Nicola and Cordone (1973). Fish were scattered from a boat moving close to the shoreline.

Inventory Procedures

Oneida Lake-type trapnets were used to obtain trout for both marking and recapture samples. Most groups did not become completely vulnerable to sampling until lengths of 15–18 cm (6–7 in.) were attained, generally in the fall at age 1+; this is the first period for which reliable point estimates of biomass were generally available. Exceptions were estimates based on drainage (Laramie/Long, 1961 year-class), or where growth was unusually rapid during the 1st yr of life (Bear/Long, 1959 year-class; Bear, 1961 year-class).

Netting took place in spring when the ponds became ice-free (late April–early May) and in late October–early November, roughly coinciding with a 6-mo ice-free period. Two to five nets were set for several days depending on the size of water and catch. In Bear Pond, the water was of sufficient clarity to electrofish the shoreline at night to supplement the sample of fish for marking.

Captured fish were processed for the usual data, given a serially numbered size 3 mandible tag and released, usually at the capture site. This mark constituted the basis for population estimation. Earlier studies were unable to detect significant effect of mandible tags on the growth of brook trout (Youngs 1958). However, the trend towards reduced recapture size of tagged fish was consistent, and in view of effects on other species, some impact on growth may be assumed although not of sufficient consequence to bias the objectives of this study.

Statistical Conventions and Procedures

Parameters for estimation of production were computed as outlined by Ricker (1958). Semiannual point estimates of numerical abundance of each strain of trout were based on recapture ratios of the cohort of fish tagged in the spring or fall inventory and recaptured during successive sampling periods, thus providing a minimum 6-mo span between marking and recapture samples. Where appropriate, ratios, observed in angling catches were also included. Each of the multiple samples of the marked to unmarked ratio in each cohort allowed an independent estimate of the population, and internal agreement in these was usually satisfactory. The "best" estimate was considered a weighted one based on the sum of the semiannual samples of trapnetting and angling, with the constraint that only first recapture from a particular cohort of tagged fish be counted; after this encounter, these fish were not tallied again:

$$\hat{N} = \frac{M\,(\Sigma[C + R])}{\Sigma R}$$

where M is the number of tags placed (or numbers recorded if fish were already tagged) in a given inventory period, C is the total catch of unmarked fish, and R the number of recaptures.

Since MC/N greatly exceeded 4 for most population estimates, no correction was made for small sample bias (Robson and Regier 1964); the ratio of recaptures to marked fish at large commonly exceeded 50% (class mean of 59% for all estimates). For ages 1–3, the estimates mostly have a 95% probability of being within 10% of the true mean.

Table 2 offers an example of the data available for the weighted or cumulative estimate for several tagged cohorts and multiple independent subestimates carried through the life span of one strain year-class.

Estimations of population size are presented in Tables 3–5 along with pertinent statistics on angling catch and growth. These were the basic data for computation of all vital statistics. The overall compatibility of successive population sizes lends additional confidence in the fidelity of the population estimates. In the 88 individual periods where ratio population estimates were possible, only nine inconsistencies developed where a following estimate was too large, all except one occurring in the overwinter period (identified by brackets in Table 3–5). These nine inconsistencies were resolved by assuming zero natural mortality between the two inventories and assignment of the lower (and earlier) of the two estimated populations.

Another convention was adopted for age-groups 4 and 5 when the number of fish remaining was low and recaptures insufficient for estimation. The numerical population was considered to be the actual number of trout in the sample increased in proportion to the cumulative unmarked to marked ratio for the cohort. Since only small numbers of fish were involved, these adjustments had only a minor effect on overall strain year-class parameters.

The several statistics leading to estimates of production followed procedures outlined by Ricker (1958) calculated on a semiannual basis. For each period the total mortality rate, a, was based on successive populations: $a = 1 - \hat{N}_1/\hat{N}_0$. For the overwinter estimate, $a = n$, the natural mortality rate. Expectation of death due to fishing, u, was computed

TABLE 2. Data available for successive population estimates of each strain-cohort showing the cumulative or best estimate for each semiannual inventory and related independent sample estimates, using Honnedaga strain, 1960 year-class, Long Pond, as example.

Date	Age	Basis for estimate	Marked at large (M)	Recaptures (R)	New fish (C)	Estimated population ($\hat{N}$)
1960 Oct.	0+	---------- Stocking ----------				350
1961 Fall	1+	Cumulative	56	41	149	260
		Spring 1962	56	7	20	216
		Angling 1962	56	9	34	268
		Fall 1962	56	15	52	250
		Spring 1963	56	9	28	230
		Angling 1963	56	13	36	211
		Fall 1963	56	11	36	244
		Spring 1964	56	5	17	246
1962 Spring	2	Cumulative	27	21	164	238
		Angling 1962	27	6	37	194
		Fall 1962	27	11	56	164
		Spring 1963	27	6	31	167
		Angling 1963	27	3	46	441
		Fall 1963	27	7	40	181
1962 Fall	2+	Cumulative	67	47	76	175
		Spring 1963	67	20	17	124
		Angling 1963	67	16	34	209
		Fall 1963	67	18	29	175
		Spring 1964	67	9	13	164
		Fall 1964	67	6	8	156
1963 Spring	3	Cumulative	37	26	87	162
		Angling 1963	37	11	38	165
		Fall 1963	37	9	38	193
		Spring 1964	37	6	16	136
1963 Fall	3+	Cumulative	47	27	19	80
		Spring 1964	47	16	6	65
		Fall 1964	47	8	6	82
		Angling 1965	47	4	3	82
1964 Spring	4	Cumulative	22	3	27	220
1964 Fall	4+	Cumulative	14	4	9	42
1965 Spring	5		4	2	2	8
1965 Fall	5+		4	0	0	
1966		None recovered				

directly by dividing catch by the preceding spring estimate. We then proceeded to obtain n for the spring–fall period by expressions (1.8), (1.3), and (1.6) of Ricker (1958), and for biomass using relationships of (1.33) and (1.37).

Two of the five experiments involved transfer of fish to a second pond for completion of observations (Bear to Long, 1959 year-class and Laramie to Long, 1961 year-class). In computing vital statistics, however, these sets of data have been treated as a continuum and rates of survival and growth applied accordingly in computations of production.

Survival

Survivorship curves shown in the top panels of Fig. 1A–C represent logarithmic plots of populations declining as a result of natural mortality only, the effect of angling having been removed by methods noted earlier. These show the consistently higher mortality rate and shorter life span of domestic strains. Few of them lived beyond age 2+. The numbers estimated remaining by the beginning of the 3rd yr of life were 10% or less in four experiments and 20% in the fifth (Bear Pond, 1961 year-class). In contrast, all wild and hybrid strains were comparatively well represented at 3 and 4 yr of age. Few fish over age 5 were observed in any groups, except the Domestic × Assinica hybrids in which 25 specimens were netted at age 6 and 6 at age 7.

Detailed individual interpretations of survival

TABLE 3. Population statistics of Domestic (Berlin), Honnedaga, and Long Pond Outlet strains of brook trout, Bear/Long and Long ponds, 1959 and 1960 year-classes. Top entries represent number and size at stocking. Angling catch shown in italics between appropriate spring–fall population estimates. R:M is experiment ratio of recaptures to marked fish at large. $\hat{N}$ in ( ) based on fish in sample expanded on basis of R:M ratio. $\hat{N}$ in [ ] based on actual data, but adjusted to immediately preceding $\hat{N}$ for computational purposes. $\hat{N}$ at age 1+ are fish actually transferred from Bear Pond, October 1960; total recoveries in the three groups were 95, 170, and 122, respectively; drainage losses considered as "angling" mortality. One domestic fish of age 6 recorded in each of 1959–60 year-class; one age 6 Honnedaga strain, 1960 year-class.

	Domestic — RV			Honnedaga — LV			Long Pond Outlet — Ad		
Age	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)
				Bear/Long ponds, 1959 year-class, June 16, 1959					
0	300	5.8	2	300	4.8	1	300	4.6	1
1	145	24.1	154	271	22.4	118	170	21.1	91
	40		*231*	*61*		*213*	*37*		*204*
1+	95	28.4	245	135	28.4	231	101	27.7	209
2	8	30.7	336	48	30.7	308	34	30.5	281
	1		*363*	*2*		*318*	*2*		*363*
				Long Pond, 1960 year-class, Nov. 14, 1960					
2+	6	33.3	426	44	34.0	454	32	34.3	408
3	(2)	33.3	322	37	35.1	417	25	34.8	372
	2		*431*	*15*		*381*	*18*		*372*
3+				20	35.3	440	(5)	34.5	404
4				14	35.1	395	(5)	34.5	327
				8		*413*	*4*		*490*
4+				(4)	33.8	408	(1)	34.8	340
5							(1)	35.8	363
5+				(3)					
R:M		50:60			73:93			64:74	
n		*.72*			*.47*			*.51*	

	Domestic — Ad			Honnedaga — LV			Long Pond Outlet — RV		
				Long Pond, 1960 year-class, Nov. 14, 1960					
0+	350	12.4	23	350	7.4	4	350	6.9	3
1	204	18.0	59						
	10		*195*	*3*		*132*	*2*		*136*
1+	168	26.4	227	260	23.4	132	313	23.4	127
2	127	27.9	227	238	26.2	172	232	26.2	168
	45		*236*	*44*		*195*	*68*		*195*
2+	51	30.0	313	175	29.7	277	118	29.2	263
3	38	30.2	295	162	30.5	277	107	30.7	281
	13		*440*	*51*		*331*	*52*		*336*
3+	(8)	33.5	435	80	32.8	386	46	32.3	363
4	(4)	33.3	467	[220]	33.5	372	35	34.0	376
				5		*417*	*2*		*499*
4+				42	34.0	422	10	34.5	417
5				(13)	33.8	367	(7)	35.3	390
				7		*408*	*3*		*376*
5+[a]				(6)	32.8	381	(3)	31.8	376
R:M		96:180			171:274			194:282	
n		*.52*			*.37*			*.37*	

TABLE 4. Population statistics of Domestic (Berlin) and Horn Lake strains of brook trout, Laramie/Long and Bear ponds, 1961 year-class. In Laramie/Long number of fish at age 1 is number actually transferred from Laramie Pond, June 1, 1962; total recoveries in two groups, 119 and 130, respectively; transfer losses considered as "angling" mortality. Other explanations given in Table 3 heading.

	Domestic — RV			Horn — Ad		
Age	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)
	Bear Pond, 1961 year-class, June 6, 1961					
0	700	6.6	3	700	4.3	1
0+	631	19.8	86	529	15.7	39
1	384	22.9	118	451	19.8	68
	142		*191*	*59*		*136*
1+	180	27.4	222	360	25.9	159
2	140	27.9	200	297	27.2	172
	90		*240*	*78*		*222*
2+	(25)	28.4	181	213	29.0	231
3	20	29.0	213	[216]	30.0	227
	8		*263*	*28*		*272*
3+	(10)	27.4	181	139	30.2	263
4	(7)			[235]	30.7	227
				23		*259*
4+	(5)	29.2	186	(31)	30.5	245
5				(2)	30.2	186
R:M		164:257			431:609	
n		*.47*			*.23*	
	Laramie/Long ponds, 1961 year-class, June 6, 1961					
0	500	6.6	3	500	4.3	1
0+	265	13.2	23	378	10.9	14
	17		*50*	*28*		*36*
1	102	17.8	50	102	15.7	36
	1		*136*			
1+	70	24.1	159	[107]	23.1	122
2	57	25.4	172	89	25.1	159
	19		*249*	*21*		*213*
2+	20	29.5	290	66	30.0	313
3	(8)	30.7	308	[180]	31.0	295
	2		*340*	*2*		*408*
3+	5	31.8	386	29	32.5	386
4	(3)	32.8	349	(29)	33.0	349
				3		*376*
4+				(9)	33.8	381
R:M		62:104			114:180	
n		*.70*			*.56*	

are not within the purview of this paper, but some comments are in order on several gross features apparent in Fig. 1. Parallel tendencies of changes in seasonal mortality are independently shown in several instances. The high overwinter mortality observed between transfer at age 1+ and the following spring in the 1959 year-class in Long Pond appears to be an exceptional situation, suspected of reflecting emigration during high water when the outlet screen may have been nonfunctional. Unusual outmigration has been noted in other local waters when transferred adult trout were involved, and it is the only plausible explanation of the high overwinter loss noted. The transfer involved in the 1961 year-class from Laramie to Long Pond was made in the spring when close field surveillance of outlet facilities was possible. Differential outmigration of pre-

TABLE 5. Population statistics of Domestic (New York), Assinica Lake, and Temiscamie strains and Domestic × Assinica hybrid brook trout, 1968 year-class. Age 6 specimens included 3 Assinica, 25 hybrid, and 4 Temiscamie; age 7 specimens, 6 hybrid and 1 Temiscamie. Other explanations given in Table 3 heading.

	Domestic — none			Assinica — Ad			Hybrid — LV			Temiscamie — RV		
Age	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)	$\hat{N}$	Mean length (*cm*)	Mean wt (*g*)
					Bay Pond — 1968 year-class — Oct. 10, 1968							
0+	2995	9.4	9	3126	8.4	4	3050	9.1	7	1351	8.4	4
1		15.5	41		14.0	27		18.0	50		14.0	27
	2		*77*				*7*		*136*	*2*		*122*
1+	333	22.4	141	476	21.1	86	987	26.2	191	88	22.1	100
2	286	25.9	231	411	27.4	213	640	35.1	481	[99]	29.5	249
	58		*349*	*31*		*354*	*242*		*572*	*30*		*367*
2+	60	30.0	308	112	34.8	358	218	38.4	585	42	34.5	349
3	28	33.5	499	[138]	38.4	522	[225]	40.4	689	[54]	36.8	449
	4		*422*	*8*		*603*	*38*		*803*	*4*		*626*
3+	(24)	33.3	367	77	41.1	630	170	41.9	694	37	39.6	581
4	(11)	34.5	426	63	42.7	708	169	43.7	844	27	40.9	662
				12		*826*	*13*		*826*	*1*		*635*
4+				51	43.2	721	113	44.7	894	24	39.6	553
5				17	42.2	585	98	44.7	794	17	42.4	644
				8		*640*	*26*		*844*	*5*		*644*
5+				(6)		685	48		821	(6)		522
R:M		39:225			180:458			389:1039			70:151	
n		*.87*			*.77*			*.53*			*.77*	

dominately domestic strains has previously been established by captures in outlet traps in Laramie Pond (Flick and Webster 1964), but is not suspected of contributing to the results observed here.

First year mortality from all four groups in Bay Pond showed a marked departure from the other data for this period, varying from about 70 to 90% (data from the Temiscamie strain were similar to Assinica strain, and are not plotted in Fig. 1C). It may be relevant that Bay Pond was the only water supporting a colony of loons. Alewives, introduced in 1969, presumably would have served in a buffer role after the first natural year-classes became established in 1970. Initially, low survival in both Canadian wild strains has been observed in other tests not reported here, so other factors may be involved as well. Natural mortality was low in all wild and hybrid groups between ages 2 and 4, however.

A summary of comparative annual natural mortality rates is provided by using successive annual population estimates upon which the survivorship curves are based. The weighted average thus obtained has some constraints in application because survival is patently not uniform with age, but it is convenient for the purpose at hand. Mortality rates of wild and hybrid groups obtained in this fashion, presented in the bottom line of Tables 3–5, were lower than the domestic group under comparison by 25 and 21, 15 and 15, 24, 14, and finally 10, 24, and 10% in five experiments.

Because all strains were subjected to similar environmental stress factors, we conclude that domestic strains lacked inherent capacity to survive or were less successful in eluding external agents of natural mortality. The data and ancillary observations argue for the former, since differential mortality occurred in the absence of piscine predators in four of the experiments reported here and elsewhere (Flick and Webster 1964), and direct observations indicated avian, mammalian, or other types of predation were negligible. The exception in Bay Pond has been noted, but here unusually high early loss also occurred in wild groups. The substantially larger size of domestic groups at planting is considered of positive survival value so that the survival values obtained are conservative in representing superior performance of wild strains.

Growth

Maximum lengths and weights attained by domestic and wild strains are not greatly different in the 1959–61 year-classes compared in Long and Bear ponds (Fig. 1 and Tables 3–5), although in all instances the apparent mean lengths attained by domestic strains were slightly smaller. Weights were more nearly the same, a reflection of the higher weight to length relation in domestic strains (Flick and Webster 1964). Domestic strains consistently reached maximum size a year earlier, but larger size at planting could easily account for this (Table 3). Wild strains caught up with domestic in size during the third growing season. Larger size may have subjected some of the faster growing domestic fish to earlier exploitation, but at the levels of angling mortality

in force, the effect on the mean size of the residual population is considered to be more theoretical than real.

The 1968 year-class in Bay Pond showed different results. The interstrain hybrid exhibited superior growth over either of the two wild or domestic strains and maximum average size of nearly 0.9 kg (about 2 lb) was substantially larger (Fig. 1C). Domestic strain fish reached the same maximum size as previously: about 33 cm (13 in.). This divergence in growth was the greatest observed in the several experiments reported here. As noted, Bay Pond was the only water in which a forage fish was involved and this factor was presumed to be of major importance, even though, given appropriate conditions, brook trout readily reach a size of 1 kg or more on invertebrate forage alone.

The growth curves suggest expected seasonal stages of rapid and slow growth in several instances. Apparently, overwinter growth in all groups in Bay Pond was substantial until senescent ages, a departure from the usual dampening of growth during fall to spring exhibited in the other waters. We believe this to be characteristic of waters where fish are an important component of the diet. The considerable loss in weight at spawning is inferred from the substantially lower spring weights of older fish and has been visually interpolated in the curves. No attempt was made to compensate for loss of biomass related to spawning activity when computing comparative gross production.

Biomass

The semiannual point estimates of standing crop were adjusted upwards to remove the effect of angling mortality (Fig. 1). Generally, this had the effect of reproducing the basic curve at a higher level, but additional modes in biomass were sometimes revealed. Wild and domestic strains showed consistent differences in the shapes of the curves. As growth between the two groups was comparable, this was essentially a reflection of higher survival in wild strains, although early size differentials are also involved. Growth also played a more influential role in Bay Pond, where hybrids at age 2+ were nearly double the average weight of other strains; this coupled with higher survival produced a biomass several times that of the other strains in the experiment.

The modal biomass in domestic strain trout occurred at age 1+ in three of the experiments, and close to this age in the other two. Biomass at age 0 through 1 generally equaled or exceeded that of the wild strains at these ages. Wild strains peaked at ages 2+ or 3+, with the exception of the 1959 year-class in Bear Pond where the maximum occurred at 1+ for all three strains; as noted, this was presumed to be a consequence of immigration following transfer. In all instances, a substantially higher biomass was maintained by wild and hybrid strains for 2 or 3 yr beyond that of domestic strains.

The hypothetical biomass is an overestimate to a degree because had fish removed by angling actually been left in the population, depression of growth and perhaps increase in natural mortality would be expected. The curves are useful here, however, as visual indices of the differences in life-span performance of the various wild, hybrid, and domestic strains.

Change Factor (k)

The instantaneous growth rate less the instantaneous mortality rate is of comparative value ("critical size" of Ricker [1958]) although interpretation and philosophy in the context of management of a sport fishery is different from a commercial one. In a sport fishery, there may be merit in regulations prolonging the bulk of a year-class beyond the age of maximum biomass, provided the k-factor remains essentially at a balance point, or if satisfactory growth and condition is maintained in the older individuals. In this report, we have examined the k-values based on growth and natural mortality as a comparative parameter, although inferences as noted above are apparent.

As expected, k-values were strongly positive in early life, and exhibited seasonal fluctuations. In domestic groups, the index fell to zero during the fall-to-spring period corresponding to ages 1+ to 2 and generally remained negative thereafter. Wild strains generally remained positive or near the balance point for 1 or 2 yr longer, or into the third and fourth growing seasons. On the basis of this criterion then, there is no merit in preserving stocks of wild fish beyond age 3+ in the Bear and Long pond series, and age 4+ in Bay Pond. The exceptional overwinter growth in Bay Pond resulted in k-values out of phase with all the other ponds.

Yield

Biomass removed by angling (Table 6) closely reflected gross production with a correlation of 0.93, excluding Bay Pond data because of difference in angling methods. Principal harvests of

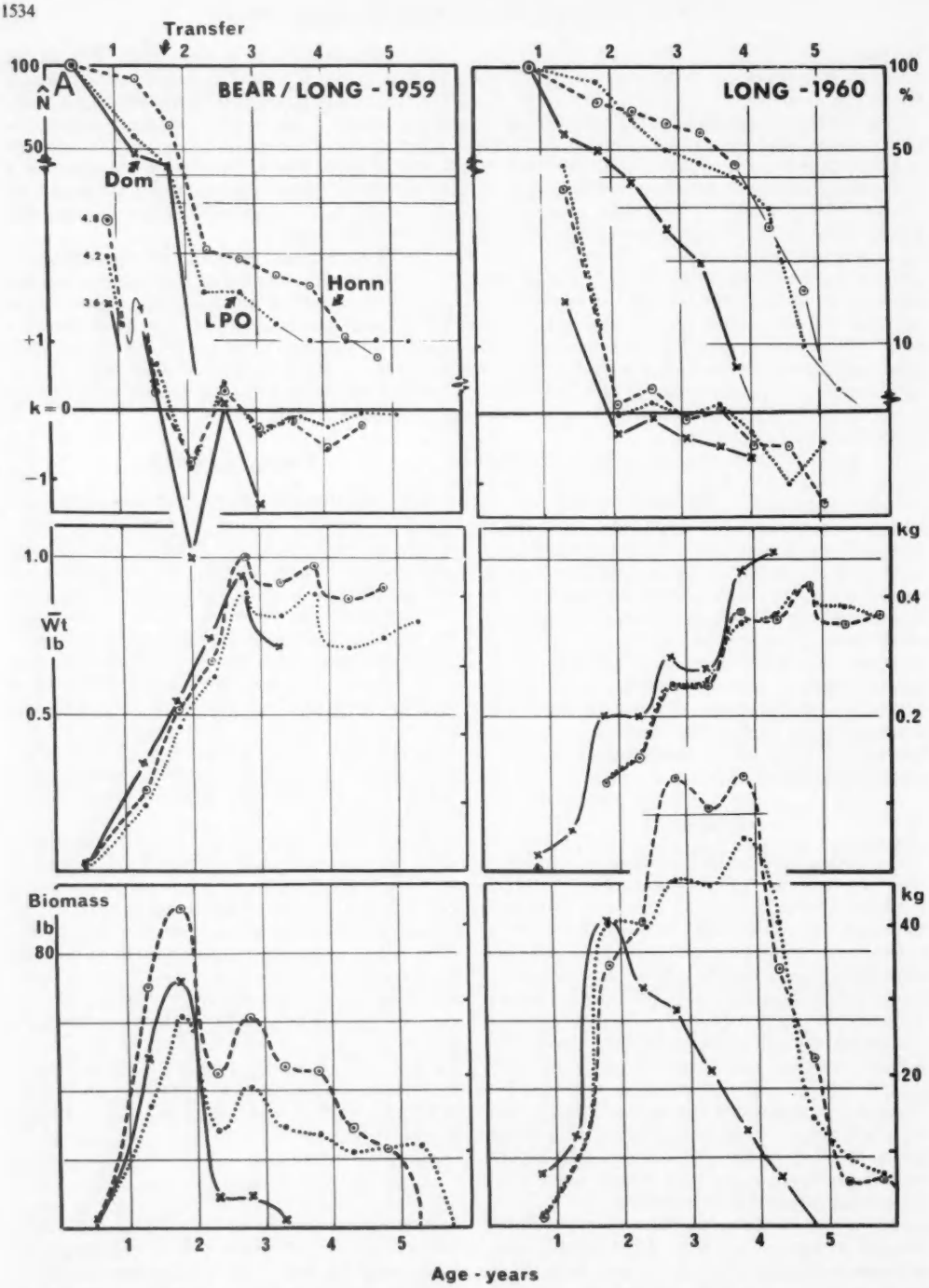
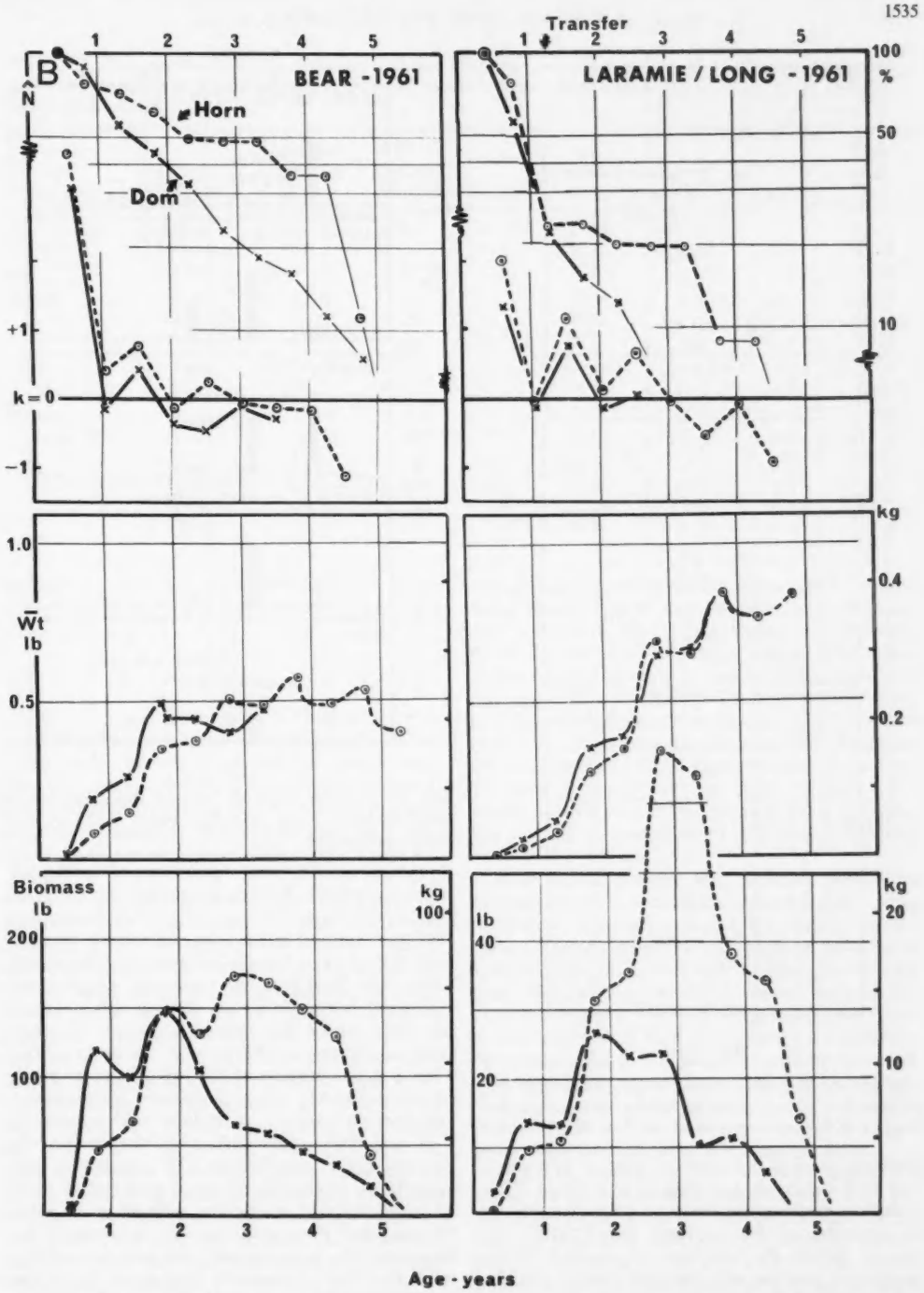


FIG. 1. Survivorship, *k*-indices, growth and biomass of A, domestic (Berlin), Honnedaga, and Long Pond Outlet strains of brook trout (*Salvelinus fontinalis*) in Bear/Long and Long ponds, 1959 and 1960 year-



classes (based on semiannual sample data given in Table 3); B, domestic (Berlin) and Horn Lake strains of brook trout in Laramie/Long and Bear ponds, 1961 year-class (based on data in Table 4); *Continued*

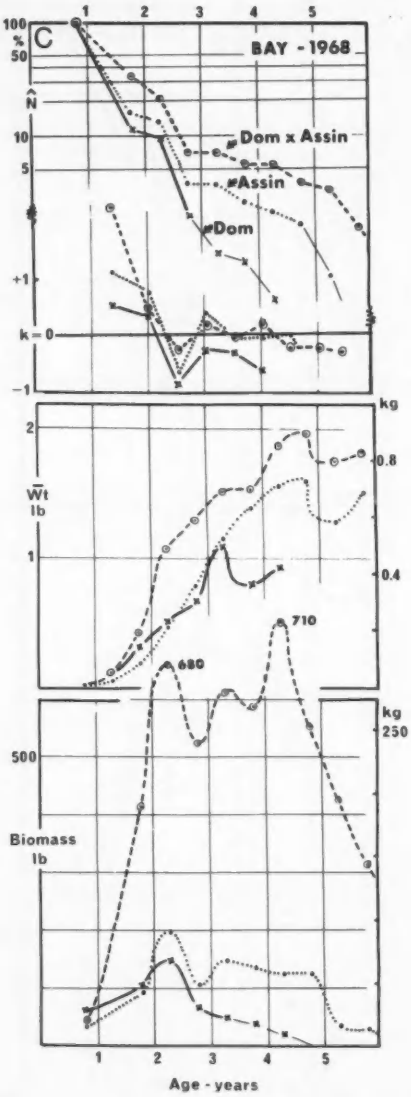


FIG. 1. C, Domestic (New York), Assinica, and Domestic × Assinica strains of brook trout in Bay Pond, 1968 year-class (based on data in Table 5).

domestic strains occurred at ages 1 and/or 2, and wild strains at 2–4 (Fig. 2 and Table 3–5). This was partly a consequence of the larger size of domestic strains in most experiments, but mainly reflects the attribute of survival. These results are identical with those of Greene (1952), although in his experiment the minimum size limit of 7 in. (17.8 cm) produced even more

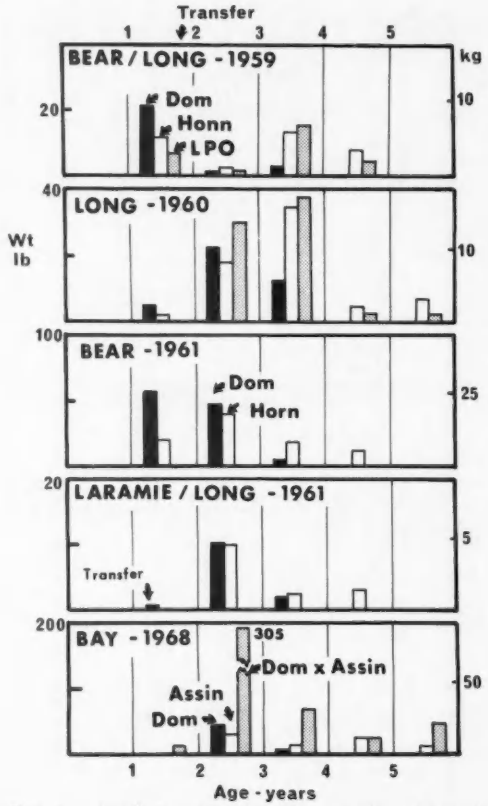


FIG. 2. Angling catch of various strains of brook trout in Bear, Long, and Bay ponds, 1959–61 and 1968 year-classes.

dramatic age-selective harvesting of wild and domestic groups. Greene compared the catch of the two strains on the basis of pounds caught per 100 fingerlings stocked. This parameter was 13 and 80% higher for the wild strain (Cranberry Lake, New York) in two successive year-classes.

Greater vulnerability to angling (fly fishing) has been noted for domestic strains in some specific instances (Flick and Webster 1962, 1964). A comparison of the regressions of catch on the estimated spring population for domestic and for wild strains yield lines with slopes of 0.37 and 0.19, respectively, but the coefficients do not differ significantly. In computing the regressions, catch data for age 1 wild strains were excluded because of the size differential in early life, and Bay Pond statistics were not considered because of the comparatively unrestricted angling methods. The substantially higher catch of the age 2 hybrid, Domestic × Assinica, in Bay Pond, may in part be due to higher vulnerability to

TABLE 6. Comparative indices for domestic, wild, and interstrain hybrid brook trout based on gross production and yield to angling in relation to number or weight stocked. Factors computed before rounding, using domestic strain values as unity.

Water and year-class	Strain	Gross production (*kg*)	Kg/unit stocked	Factor	Wt stocked (*kg*)	Kg/kg stocked	Factor	Total catch (*kg*)
Bear/Long	Dom	42.2	0.14	1	0.62	68	1	10.5
1959	Honn	72.1	0.24	1.7	0.27	269	4.0	22.8
	LPO	44.4	0.15	1.1	0.23	192	2.8	16.8
Long	Dom	52.6	0.15	1	7.94	6.6	1	18.2
1960	Honn	88.0	0.25	1.7	1.33	66.0	10.0	30.8
	LPO	87.5	0.25	1.7	1.11	78.8	11.9	33.1
Bear	Dom	93.4	0.13	1	2.29	41	1	50.8
1961	Horn	100.2	0.14	1.1	0.57	176	4.3	38.9
Laramie/	Dom	26.8	0.054	1	1.63	16	1	5.5
Long 1961	Horn	42.2	0.084	1.6	0.40	105	6.6	7.5
Bay	Dom	120.2	0.040	1	27.17	4.4	1	22.0
1968	Assin	185.1	0.059	1.5	13.61	13.6	3.1	30.8
	Hybrid	609.6	0.200	5.0	20.46	29.8	6.8	204.3
	Temis	52.6	0.039	1.0	6.08	8.7	2.0	17.6

angling, but this is confounded with the larger size of the hybrid and the possibility of some selection by anglers.

Conclusions

Higher survival and consequent effects on biomass and yield resulted in consistently better performance of wild and hybrid strains over domestic strains under the conditions presented. The comparison may be carried further to more concisely summarize the relationship and provide a basis for economic evaluation (Table 6).

Gross production per recruit (i.e. per unit stocked) permits adjustment for differences in the number of fish stocked in each strain and allows a degree of comparison between experiments, although other variables are involved for interpretation in terms of production or stock density per se. In 9 of the 14 observations, gross production was between 0.13 and 0.25 kg/recruit stocked; wild groups had a life-span gross production averaging 0.157 kg compared with 0.105 for wild strains, 50% greater. In three of the experiments, one of the wild strains had about the same index as domestic, but this was the result of biomass elaborated at an early age by the domestic stock and was largely lost to natural causes by the end of the 3rd yr of life. Yield per recruit does not take into account the substantial size differences that existed between domestic and wild strains at stocking.

These experiments demonstrated that size does not play an overriding role in shaping survival among the groups compared here. Other factors being equal, it costs more to rear larger fish, so that economics should play a role in evaluating the biological data presented. Gross production weight stocked ratio provides an index useful in making such a judgment. The comparative factors reduce the biomass elaborated to a common denominator, as well as reflect growth and survival parameters. These ratios ranged from 2 to 12 times (average 5.7) as much biomass produced by wild and hybrid strains. They are subject to adjustment due to differential rearing costs if they exist.

Wild strains present more cultural difficulties because hatchery techniques and diets have been developed in large measure for highly inbred lines of trout. Wildness and perhaps traditional artificial diets may contribute to slow growth and poor hatchery performance (when judged by domestic strains), but size alone is obviously not a valid criterion of field performance. Availability or maintenance of a dependable wild brood stock may also be an important added cost consideration, and greater susceptibility of wild strains to disease while in the hatchery can be a major production problem in a wild trout program.

None of the above considerations appear to constitute insurmountable problems and the substantially higher returns from wild strains argue that any increased difficulties in handling should not be overriding. Native wild strains merit greater attention than customarily given in most trout management programs currently in effect (Greene 1952; Behnke 1972). Possible benefits

of capitalizing on the "lost" attributes of native or introduced wild strains and especially the potential of interstrain hybrids should not be overlooked.

The interstrain hybrid involved in the experiment at Bay Pond was singular in performance in what appears to be an expression of hybrid vigor. This and other Canadian hybrids currently under evaluation offer promise of providing a superior fish for growth and survival in natural waters where an objective of management is not preservation of an indigenous or introduced wild strain.

In earlier observations on hatchery and field performance of interstrain hybrids using native New York wild strains of brook trout and a domestic strain, results were not as spectacular. Tyler (1964) noted intermediate hatchery growth in the interstrain hybrid, but it was closer to the domestic parent, especially in length. Evaluation of performance of these fish was only partial, but the size of the hybrids at ages 1 and 2+ equaled or exceeded domestic strains (Flick and Webster 1965). The possibility of greater diversity between the gene pool of the Canadian and the New York domestic strain is speculative, but merits further study.

Efforts to explore the potential of interstrain hybrid trout have been limited. Donaldson et al. (1957) presented data on growth and angling catch of domestic × wild *Salmo clarkii*; hatchery and lake growth following planting was similar, but hybrids showed higher weight representation in the catch in one planting and was intermediate between the parents in a second. Leon (1971) field tested hybrids between an inbred domesticated rainbow trout and steelhead trout (*Salmo gairdneri*). Despite more rapid hatchery growth of the rainbow strain, hybrids showed higher survival as measured by yield to anglers (or possibly the hybrids were more vulnerable to angling). He concluded that the hybrid had definite positive management attributes when stocked in appropriate waters.

The above analysis indicates that wild and hybrid strains offer significant economic benefits under the conditions of management described for these experiments: moderate levels of exploitation (annual forces of fishing of 20–30%), and a minimum size giving protection through at least one full growing season following planting as fall fingerlings. These restrictions are not without possible consequences, however, since reduced exploitation combined with unduly successful natural reproduction can be expected to depress growth rates, perhaps to a point where few fish reach minimum legal size. While natural reproduction may be desirable under some circumstances, control of recruitment through annual planting has advantages for small lakes and ponds under intensive management. Reduced size and bag limits imply release of a substantial number of fish caught so that gear restrictions will be required to minimize hooking mortality. Thus the analysis presented here, while adequate for comparative purposes, is simplistic in terms of the management concerns noted above.

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The cooperation and financial support of the late Mr D. P. Ross and Mrs Ross and the late Mr W. Rockefeller have in large measure made this series of experiments possible. The Bureau of Sport Fisheries and Wildlife (Federal Fish Hatchery, Cortland, New York) and the Bureau of Fish, New York State Department of Environmental Conservation (especially Mr R. Griffiths and Mr I. Annis of the Fish Propagation Unit) have provided fish and collaborated in other ways. Special acknowledgment is made to the Department of Tourism, Province of Quebec, who through Dr E. Corbeil, and earlier Dr V. Legendre, made it possible to obtain eggs from Canadian strains of trout in the James Bay area.

A large number of former graduate students in the Department of Natural Resources, Cornell University, participated in various ways, as did a support staff of technical help. Additional special acknowledgment must be made to the late Mr C. W. Lyons Jr., whose dedication as fish culturist contributed materially to the rearing program of wild trout in the early experiments. Mrs B. Little was responsible for much of the computational work. We appreciate the helpful editorial suggestions made by our colleagues Drs W. H. Everhart, W. D. Youngs, and C. D. Lowe.

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Effect of Temperature and Salinity on Extension of Siphons by *Mercenaria mercenaria*[1]

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VAN WINKLE, W., S. Y. FENG, AND H. H. HASKIN. 1976. Effect of temperature and salinity on extension of siphons by *Mercenaria mercenaria*. J. Fish. Res. Board Can. 33: 1540–1546.

Extension of siphons was used as a criterion of activity to examine the response of the quahog clam, *Mercenaria mercenaria*, to various combinations of test and acclimation temperatures and salinities. A quadratic regression model for the percentage of clams active as a function of the test temperature and salinity was assumed, and response surface contours for various percentages of activity were calculated and plotted.

The regression model accounted for 72–88% of the observed variability in the 13 experiments considered. The contours are hyperbolic instead of elliptical for five of the experiments; no biologically meaningful estimates of the lower and upper temperature and salinity limits can be obtained in such cases. Low levels of activity, even at optimal T–S combinations, occurred during the summer. Some of the observed shifts in the position and shape of the temperature–salinity response surfaces were expected in light of shifts in acclimation temperature or salinity. Other shifts in response surface could not be accounted for. The implications of these results for the purification of quahog clams harvested from polluted waters are discussed.

VAN WINKLE, W., S. Y. FENG, AND H. H. HASKIN. 1976. Effect of temperature and salinity on extension of siphons by *Mercenaria mercenaria*. J. Fish. Res. Board Can. 33: 1540–1546.

Les auteurs utilisent l'extension des siphons comme critère d'activité dans l'analyse de la réponse de la palourde, *Mercenaria mercenaria*, à diverses combinaisons de températures et de salinités d'essai et d'acclimatation. Ils supposent un modèle de régression quadratique pour le pourcentage de palourdes actives comme fonction de la température et de la salinité d'essai, et ils calculent et portent sur graphiques les coutours de surface de réponse pour divers pourcentages d'activité.

Le modèle de régression s'accorde avec 72–88% de la variabilité observée dans les 13 expériences effectuées. Dans cinq de ces expériences, les contours sont hyperboliques plutôt qu'elliptiques; dans de tels cas, on ne peut obtenir d'estimés biologiquement significatifs des limites inférieures et supérieures de température et de salinité. En été, les niveaux d'activité sont bas, même à des combinaisons optimales de T–S. Quelques-uns des déplacements observés dans la position et la forme des surfaces de réponse à la température et à la salinité avaient été anticipées à la lumière des déplacements de la température ou de la salinité d'acclimatation. D'autres changements dans la surface de réponse demeurent inexpliqués. Les auteurs discutent des implications de ces résultats en regard de la purification des palourdes récoltées dans des eaux polluées.

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THE quahog clam, *Mercenaria mercenaria*, is eurythermal as indicated by its distribution along the Atlantic coast from the Gulf of St. Lawrence to Florida. Ansell (1968) concluded that *M. mercenaria* grows fastest at 20 C and that below 9 and above 31 C growth ceases. Both field and laboratory studies (Castagna and Chanley 1966; Hamwi 1969; Hamwi and Haskin 1969; Van

TABLE 1. Sites and dates of collection and experimentation and conditions of temperature and salinity acclimation for *Mercenaria mercenaria*.

Expt no.	Stock	Date of collection	Date of experiment	Acclimation conditions
1	DB	Apr. 20, 1964	Apr. 24–May 4, 1964	10–15 C; 19–22‰
2	DB	May 22, 1964	May 26–31, 1964	15–19 C; 21–22‰
3	GS[a]	Apr. 20, 1964	Apr. 24–May 4, 1964	10–15 C; 19–22‰
4	GS[a]	May 22, 1964	May 26–31, 1964	15–19 C; 21–22‰
5	SHB	Mar. 20, 1965	Mar. 22–30, 1965	5–10 C; 17–20‰
6	SHB	Mar. 20, 1965	Aug. 25–Sept. 9, 1965	25–28 C; 22–28‰
7	SHB	Mar. 20, 1965	July 6–13, 1966	15 C; 24‰
8	SHB	July 25, 1966	Aug. 4–12, 1966	24–26 C; 26–28‰
9	SHB	July 25, 1966	Aug. 26–Sept. 2, 1966	25–28 C; 26–28‰
10	DB	Sept. 18, 1965	Sept. 21–29, 1965	25–28 C; 24–28‰
11	DB	Sept. 18, 1965	Mar. 14–18, 1966	5–6 C; 17–22‰
12	DB	Sept. 18, 1965	July 26–Aug. 2, 1966	10–15 C; 27‰
13	DB	Sept. 18, 1965	Aug. 16–23, 1966	25–28 C; 26–28‰

[a]The Great Sound (GS) stock was purchased and planted at the Cape Shore tidal flats in Delaware Bay, New Jersey on Sept. 13, 1963.

Winkle 1972; Wells 1961) suggest that *M. mercenaria* is only moderately euryhaline because it is rarely found below 15‰ salinity, and physiological processes, such as growth, pumping rate, and ciliary activity, are appreciably reduced at salinities below approximately 20‰.

The objective of the present study was to examine the extension of siphons by *M. mercenaria* in the laboratory at various combinations of temperature and salinity and to assess variation in this response among stocks with differing acclimation temperatures and salinities. This study was conducted with the longer-range objective of defining temperature and salinity limits necessary for the purification (i.e. depuration) of quahog clams harvested from polluted waters. Any set of temperature and salinity limits does not necessarily define conditions that are sufficient for depuration. Quahog clam activity and self-cleansing are influenced by other factors, as well, such as turbidity and reproductive condition.

Materials and Methods

Mercenaria mercenaria were obtained from the following three locations in New Jersey, where, at the time of these experiments, quahog clams were being commercially harvested: Delaware Bay (DB), Sandy Hook Bay (SHB), and Great Sound (GS) on the ocean side of Cape May. Information on the sites and dates of collection and experimentation, as well as conditions of temperature and salinity acclimation, if any, are summarized in Table 1.

To determine the temperature and salinity optima, the extension of siphons of the three stocks was monitored during spring, summer, and fall at five or six approximately equally spaced levels of test salinity (e.g. 15, 20, 25, 30, 35, and 40 ‰) and five approximately equally spaced levels of test temperature (e.g. 10, 15, 20, 25, and 30 C). Test salinities (±1‰) were obtained by either diluting the natural sea water with aged tap water or adding an appropriate amount of artificial sea salt. Test temperatures were thermostatically controlled to within ±1.0 C. Choice of the lower levels of test temperature and test salinity (Table 2) were based upon results of preliminary experiments that showed either low or no activity under these conditions. The upper levels of test temperature and salinity (Table 2) selected were higher than the maximum levels commonly occurring in the field where the clams were collected.

Extension of siphons was used as the criterion of clam activity. Groups of ca. 50 clams were bathed in 20 liters of sea water of known salinity in a glazed earthenware tank (static system). Clam activity was monitored during an 8-h period (0830–1630) by noting on an hourly basis the number of clams with siphons extended. Hourly observations, as opposed to more frequent observations, seemed adequate because individual clams commonly extended their siphons or remained closed for hours at a time. The siphons were classified as extended if the siphons protruded beyond the edge of the valves and were open. The numbers of hours of clam activity for the period were totaled, and the percent activity was calculated as:

$$\% \text{ clam activity} = \frac{\text{Observed number of active clam hours}}{\text{Total possible number of active clam hours}} \times 100$$

When the monitoring of clam activity was concluded at the end of an 8-h period, the clams were removed from the five tanks and placed in a flow-through tank at the acclimation (ambient) temperature and salinity (Table 1). The earthenware tanks were

TABLE 2. Lower salinity limit (S_l), upper salinity limit (S_u), lower temperature limit (T_l), and upper temperature limit (T_u) for the 20, 50, and 80% contours predicted by the quadratic response surface model; the area enclosed by these three contours is also given. The lower and upper test temperature and salinity limits are included as guidelines to discourage extrapolation beyond temperature–salinity combinations actually used.

Expt no.	Test limits				20% Contour					50% Contour					80% Contour				
	S_l (‰)	S_u (‰)	T_l (°C)	T_u (°C)	S_l (‰)	S_u (‰)	T_l (°C)	T_u (°C)	Area (°C ‰)	S_l (‰)	S_u (‰)	T_l (°C)	T_u (°C)	Area (°C ‰)	S_l (‰)	S_u (‰)	T_l (°C)	T_u (°C)	Area (°C ‰)
1	15.5	35.7	4.9	25.4	17	38	0[b]	33[b]	544	20	36	4	29[b]	302	24	32	11	22	58
2	15.0	35.6	5.0	25.0	16	37	2	>35[b]	569	19	34	9	>35[b]	343	23	29	18	30[b]	59
3	15.5	35.7	4.9	25.4	16	40[b]	4	32[b]	524	19	38	6	29[b]	334	22	35	10	25	140
4	15.0	35.6	5.0	25.0	16	37	4	33[b]	461	19	34	8	29[b]	249	23	30	14	23	38
5	15.3	40.0	9.9	29.8	14	39	4[b]	34[b]	569	17	35	9	29	278	[c]				
6	16.8	40.3	7.1	24.3	20	42	5	25	338	26	36	10	19	69	[c]				
7[a]	14.8	40.8	10.1	31.2															
8[a]	15.5	42.9	9.6	30.4															
9[a]	15.1	44.3	10.6	30.7															
10	19.9	39.5	9.2	30.5	21	42	*b*	34[b]	541	24	39	*b*	26	312	29	34	c	c	44
11	15.0	35.1	10.0	29.9	15	37	0[b]	>35[b]	629	18	34	6[b]	35[b]	348	[c]				
12[a]	14.7	39.2	9.0	30.5															
13[a]	15.4	38.9	9.5	30.5															

[a]Hyperbolic contours; no biologically meaningful estimates of lower and upper salinity and temperature limits can be obtained from the response surface.
[b]Beyond range of test salinity or temperature by more than 3‰ or 3 C degrees.
[c]Predicted values did not get this high.

drained and refilled with freshly prepared sea water of the next test salinity. The following morning clams were again placed in the tanks at each of the five test temperatures and after ½ h, monitoring of clam activity resumed. This procedure was repeated each day until tests at each of the five or six salinities had been completed. Photoperiod was not carefully controlled.

A 5 × 5 or 5 × 6 factorial design was used, with five levels of temperature and five or six levels of salinity for a total of 25 or 30 temperature–salinity combinations. The dependence of percentage activity on temperature and salinity was approximated by the general quadratic model for two independent variables (Costlow et al. [1960, 1962]):

$$Y = b_0 + b_1T + b_2S + b_3T^2 + b_4S^2 + b_5TS$$

where Y = arcsin $\sqrt{\text{percent activity}/100}$, T = temperature (C), S = salinity (‰).

The estimates of the regression coefficients were calculated by the method of least squares from the observed percentage activity values at the 25 or 30 temperature–salinity combinations. A separate equation was obtained for each experiment. By using this method of analysis it was possible to predict percentage activity at temperature–salinity combinations in addition to those actually used in the laboratory. However, care has been taken to restrict predictions to the ranges of temperatures and salinities actually used.

Response surface contours for selected percentages of activity were calculated and plotted. Lower and upper temperature and salinity limits were estimated by measuring tangents to the 20, 50, and 80% contours, as indicated in Fig. 1 for the 20% contour. Limits were estimated for the 50 and 80% contours when these contours were present. In addition, the areas within the 20, 50, and 80% contours were measured with a planimeter. These areas provide an integrated measure of the combined effects of temperature and salinity on siphon extension.

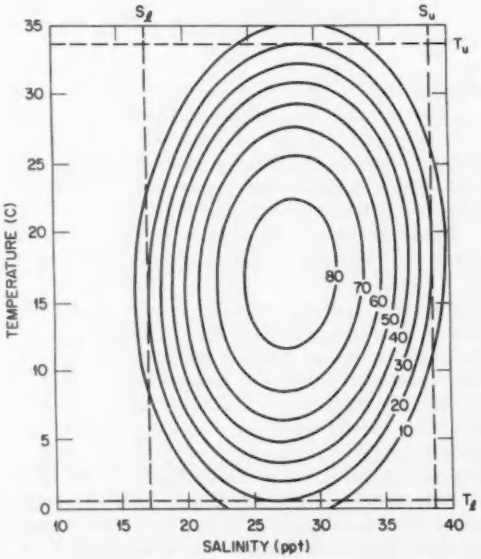

FIG. 1. Predicted response surface for percentage activity based on observed activity at 25 temperature–salinity combinations for the quahog clam, *Mercenaria mercenaria*, from Delaware Bay, New Jersey (experiment 1). S_l = lower salinity limit; S_u = upper salinity limit; T_l = lower temperature limit; T_u = upper temperature limit, all for the 20% activity contour.

Results

Results from 13 experiments are summarized in Tables 2 and 3. The number of clams used, the coefficient of determination (r^2), and the six regression coefficients (b_i) for the quadratic response surface model are given in Table 3. The

TABLE 3. Sample size (N), coefficient of determination (r^2), and regression coefficients (b_i) and associated standard errors (in parentheses) for the quadratic response surface model.

Expt no.	N	r^2	b_0	b_1	b_2	$b_3 \times 10^4$	$b_4 \times 10^4$	$b_5 \times 10^4$
1	25	0.77	−4.06	0.070	0.334	−26.3	−62.3	7.2
			(0.76)	(0.040)	(0.055)	(10.4)	(10.4)	(8.9)
2	25	0.84	−3.58	0.049	0.313	−15.2	−63.7	9.3
			(0.58)	(0.030)	(0.043)	(8.1)	(8.0)	(6.7)
3	25	0.76	−4.14	0.107	0.320	−43.9	−62.4	18.5
			(0.95)	(0.050)	(0.068)	(13.0)	(12.9)	(11.1)
4	25	0.84	−4.15	0.097	0.331	−33.3	−66.5	11.0
			(0.66)	(0.034)	(0.048)	(9.2)	(9.1)	(7.6)
5	30	0.76	−2.88	0.118	0.214	−28.8	−39.9	−2.2
			(0.57)	(0.037)	(0.032)	(8.3)	(5.4)	(5.4)
6	35	0.86	−3.49	0.132	0.217	−35.4	−32.7	−8.9
			(0.39)	(0.030)	(0.021)	(7.5)	(3.3)	(4.6)
7	30	0.83	−1.12	−0.060	0.144	12.9	−25.4	4.7
			(0.34)	(0.022)	(0.018)	(4.7)	(3.0)	(3.4)
8	30	0.83	−2.02	0.004	0.170	1.3	−25.5	−5.6
			(0.36)	(0.021)	(0.019)	(4.6)	(2.9)	(3.4)
9	30	0.79	−1.22	−0.030	0.147	6.1	−25.3	−0.5
			(0.33)	(0.023)	(0.017)	(5.2)	(2.9)	(3.7)
10	35	0.88	−5.35	0.020	0.409	−6.8	−64.2	−5.3
			(0.59)	(0.026)	(0.036)	(5.6)	(6.0)	(5.0)
11	25	0.72	−3.28	0.073	0.276	−15.7	−51.8	−2.5
			(0.67)	(0.038)	(0.042)	(8.7)	(8.1)	(7.3)
12	30	0.85	−0.68	−0.062	0.114	15.6	−17.6	−2.1
			(0.27)	(0.016)	(0.015)	(3.5)	(2.6)	(2.7)
13	30	0.85	−1.12	−0.027	0.122	6.8	−17.9	−4.3
			(0.28)	(0.017)	(0.017)	(3.8)	(3.0)	(2.9)

r^2 values indicate that the model accounts for 72–88% of the observed variability (Table 3). The lower and upper salinity and temperature limits for the 20, 50, and 80% contours and the areas enclosed by each of these contours are presented in Table 2. The lower and upper test temperature and salinity limits are given also as guidelines to discourage extrapolation (Table 2).

The contours are hyperbolic instead of elliptical for experiments 7–9 and 12–13; the response surface for experiment 7 (SHB stock during the summer) is an example (Fig. 2). The hyperbolic contours in all five cases appear to be a result of low percentage activity values with little variation. In fact, the three highest observed percentage activities for these five experiments were 42, 51, and 54%. Because the number of test temperature–salinity combinations proved to be inadequate to describe the response surface satisfactorily, no biologically meaningful estimates of lower and upper salinity and temperature limits and associated areas can be obtained (Table 2 and Fig. 2). Costlow et al. (1960, 1962) obtained hyperbolic contours also but did not point out that they are most likely a statistical artifact due to low percentage activity values with little variation.

In the present study, the lowest levels of activity, even at optimal temperature–salinity combinations, occurred during the summer. The dates for experiments 7–9 and 12–13 cover the period July 6–September 2, which with one exception (experiment 6, August 25–September 9) did not overlap with the dates for the other 10 experiments (Table 1).

The results from two pairs of experiments were selected for further analysis. Figure 3 illustrates the response surfaces for the DB stock during midspring (April 24–May 4; experiment 1) and late spring (May 26–May 31; experiment 2). The primary change in the acclimation conditions between experiments was an increase in water temperature from 10 to 15 C to 15 to 19 C (Table 1). Corresponding to this increase in temperature, there was a marked shift in the position of the response surface towards warmer temperatures with little change in the position of the response surface relative to the salinity axis (Table 2 and Fig. 3). Specifically, the lower and upper salinity limits shifted 3‰ or less (20, 50,

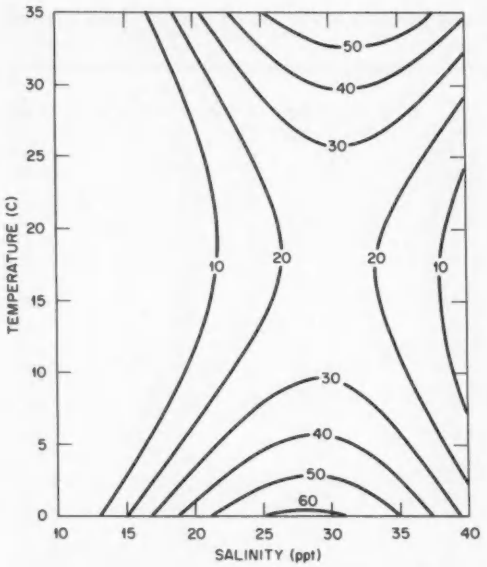

FIG. 2. Predicted response surface for percentage activity based on observed activity at 30 temperature–salinity combinations for *M. mercenaria*, from Sandy Hook Bay, New Jersey (experiment 7).

and 80% contours), while the lower and upper temperature limits shifted upwards 5–8 C (50 and 80% contours). The upper temperature limits for the 20 and 50% contours were beyond the range of test temperatures by more than 3 C degrees (Table 2), and thus, they must be viewed with caution in documenting the shift in the response surface. The areas inside the three contours were slightly greater during late spring than midspring (Table 2).

Figure 4 illustrates the response surfaces for the SHB stock in March (5–10 C and 17–20‰) and the following August–September (25–28 C and 22–28‰) (see Table 1, experiments 5 and 6). Thus, for this pair of experiments both the acclimation temperature and the acclimation salinity increased appreciably between late winter and late summer. There was a corresponding upward shift in the lower and upper salinity limits, particularly the lower salinity limits (more than a 5‰ increase for the 20 and 50% contours; see Table 2). Instead of the expected increase in the temperature limits, however, there was a pronounced decrease in the upper temperature limits (approx. 10 C degrees decrease for the 20 and 50% contours in late summer as compared to late winter [Fig. 4 and Table 2]).

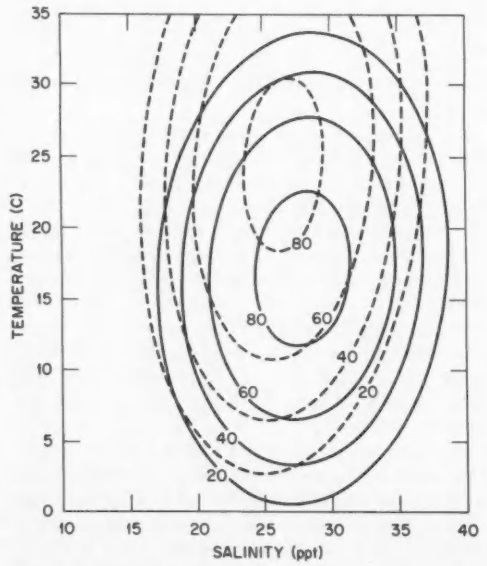

FIG. 3. Predicted response surface for percentage activity based on observed activity at 25 temperature–salinity combinations for *M. mercenaria*, from Delaware Bay, New Jersey during April 24–May 4, 1964 (experiment 1, solid) and May 26–31, 1964 (experiment 2, dashed).

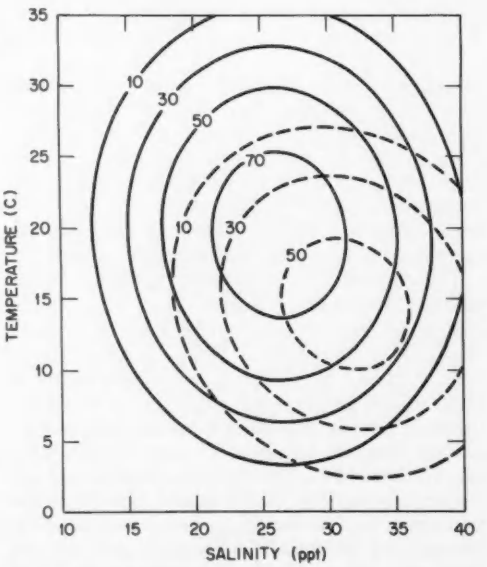

FIG. 4. Predicted response surface for percentage activity based on observed activity at 30 temperature–salinity combinations for *M. mercenaria*, from Sandy Hook Bay, New Jersey during March 22–30, 1965 (experiment 5, solid) and August 25–September 9, 1965 (experiment 6, dashed).

Discussion

Extension of siphons by *M. merceneria* and by several other commercially important bivalve species is a necessary condition for pumping, which is, in turn, a necessary condition for feeding, respiration, and purification. Although extension of siphons is a crude index of activity, experiments using this index of activity can be done quickly, easily, and inexpensively. Thus, use of this index can be of considerable value in initially defining limits for temperature, salinity, and even other variables (such as photoperiod, food, and turbidity) to be used in depuration of quahog clams and other shellfish. In addition, the results of such studies provide guidelines for more detailed and sophisticated studies on activity and purification (Hamwi 1969; Canzonier 1971).

The set of physiological characteristics determining the temperature–salinity response surface for extension of siphons illustrates considerable phenotypic plasticity with respect to acclimation temperature, acclimation salinity, and reproductive condition. Temperature limits shifted upward from April to May (Fig. 3). Salinity limits also shifted upward from late winter to late summer (Fig. 4), presumably due to an increase in the acclimation salinity from late winter to late summer. Relatively low levels of activity predominated in the summer, possibly associated with spawning earlier in the summer or seasonal changes in water quality or food (Fig. 2).

Not all of the shifts in the response surfaces would be expected on the basis of the shifts in acclimation temperature and salinity, e.g. the pronounced decrease in the upper temperature limit associated with an increase in the acclimation temperature (Fig. 4). This type of unexpected change indicates that the effects on activity of other water quality parameters and of the physiological state of the quahog clams must be investigated in setting up optimum conditions for purification. This decrease in activity at high summer temperatures is consistent with previous observations in New Jersey coastal waters of decreased growth rate in the summer as compared with spring and fall (Haskin 1954).

There did not appear to be systematic differences among the DB, SHB, and GS stocks (Tables 1 and 2), although detection of other than major differences would require further experimentation.

The results of these experiments suggest temperature and salinity limits that are necessary (although not sufficient by themselves, because other factors influence activity) for the purification of quahog clams. As indicated by previous studies (Hamwi 1969; Wells 1961), *M. mercenaria* is only moderately euryhaline. Purification of quahog clams should not be considered at salinities below 20‰ and is likely to be most successful at salinities above 22–23‰ (Table 2).

Although no experiments were conducted during the winter months (December–February), the two March experiments (experiments 5 and 11, Table 1) suggest that purification of quahog clams should not be considered at temperatures below 10 C (Table 2). The use of heated water in the winter should be explored. The results of the spring and fall experiments (experiments 1–4 and 10, Table 1) suggest that purification of hard clams should not be considered at temperatures above 30 C and are likely to be most successful at temperatures of 25 C and below (Table 2). The results of the summer experiments (experiments 6–9 and 12–13, Table 1) suggest that it may be difficult to purify quahog clams during the months of June–August, regardless of the temperature and salinity conditions (Table 2). Further studies in the Rutgers Shellfish Research Laboratory (unpublished data), using *Escherichia coli* as an index to purification, have led to conclusions that depuration of quahog clams should not be attempted when activity levels drop below 50%.

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Azygokeras columbiae, a New Genus and Species of Marine Epibenthic Copepod (Calanoida: Aetideidae) from British Columbia

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KOELLER, P. A., AND J. L. LITTLEPAGE. 1976. *Azygokeras columbiae*, a new genus and species of marine epibenthic copepod (Calanoida: Aetideidae) from British Columbia. J. Fish. Res. Board Can. 33: 1547–1552.

Azygokeras columbiae n.gen., n.sp. can be distinguished from other genera of Aetideidae by the asymmetrical first antennae of the male, the setation of the first two segments of the second antennal exopod of the female, and by the spinulation on basipods and rami of the swimming legs of both sexes. The animal was found only in deep hauls from Bute Inlet and is probably an epibenthic form.

KOELLER, P. A., AND J. L. LITTLEPAGE. 1976. *Azygokeras columbiae*, a new genus and species of marine epibenthic copepod (Calanoida: Aetideidae) from British Columbia. J. Fish. Res. Board Can. 33: 1547–1552.

Azygokeras columbiae n.gen., n.sp., se distingue des autres genres d'Aetideidae par les premières antennes asymétriques du mâle, la disposition des soies des deux premiers segments du deuxième exopode antennal de la femelle et la disposition des spinules sur les basipodes et les rames des pattes natatoires des deux sexes. L'animal n'a été trouvé que dans les profondeurs de l'inlet Bute et est probablement une forme épibenthique.

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Azygokeras columbiae n.gen., n.sp. was found in plankton samples taken during an investigation of deep-living inlet fauna conducted at the University of Victoria in 1972–73. In vertical series it was always most abundant in the depth interval closest to the bottom of Bute Inlet (maximum depth 650 m) and could therefore belong to a bottom-living copepod fauna. Such a fauna has been shown to exist elsewhere (Bradford 1969; Grice and Hulseman 1970; Grice 1972). The animal was never observed in collections obtained from above 300 m in Bute Inlet and was absent from deep hauls taken in several other B.C. inlets and in the Strait of Georgia.

The family Aetideidae consists of many genera which are both taxonomically distant and ecologically distinct. Many species still have an obscure systematic position. Some species are totally pelagic while others are associated with the seabottom to varying degrees (Mathews 1964). The epibenthic fauna has yet to be investigated in many areas and the present world collection may contain only a fraction of the total genera of Aetideidae in existence. The asymmetry of the male first antennae of *A. columbiae* n.gen., n.sp. is an important character new to the description of the family given by Brodskii (1950). Agreement with other familial traits justifies placing the genus within the Aetideidae.

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Materials and Methods

Specimens of *Azygokeras columbiae* n.gen., n.sp. were found among 150 net samples examined from 11 mainland inlets and adjacent waters. Samples were collected with vertical closing nets of the Juday type (0.44 m^2 mouth area, mesh size 333 μ) from the following depth intervals: 600–400, 400–300, 300–200, 200–100, 100–50, and 50–0 m. Some samples examined were collected with an obliquely hauled meter net (mesh 333 μ) or a vertically hauled SCOR net (mesh 351 μ).

All specimens were preserved in about 5% formalin solution. Microscope slide mounts of dissected

appendages and whole copepods were prepared using TURTOX CMC-S mounting medium. All identifications, drawings, and measurements were made from these slides.

Azygokeras n.gen.

Type species — *Azygokeras columbiae* n.sp., by original designation.

Etymology — Azygo- "unpaired," keras- "horns," referring to the male first antennae.

Definition — Head and first thoracic segment fused, fourth and fifth thoracic segments separate. Posterior thoracic segment reduced, produced into acute points posterolaterally. Rostrum absent. Posterior borders of abdominal segments fringed with fine spinules. First antenna with 24 segments in female, bearing numerous long annulate setae distally. First antennae of male slightly asymmetrical; right antenna somewhat stouter distally and bent backward at about third segment from end. Second antennae with endopods and exopods equal. Mandibular palp large, endopod small. First inner lobe of first maxilla with 11 spines and setae. Male mouth parts reduced. Maxillipeds massive and conspicuous in females, more slender in males. Endopod of first swimming legs 1-segmented, of second leg 2-segmented, all other rami of swimming legs 3-segmented. External spine on proximal joint of exopod of first leg present. Posterior surface of endopods of second to fourth legs spinulated, spinules on fourth legs much finer and more numerous than on second and third legs. Spinules also present on external margin of first basipod of second and third swimming legs. Fifth swimming legs of male biramous and asymmetrical, endopods 1-segmented and rudimentary.

Azygokeras columbiae n.sp.

Holotype — National Museum of Canada (NMC) No. 15614. Location, Bute Inlet, British Columbia, 50°27′N; 125°04.5′W. Depth, 600–400 m. Date collected, February 21, 1973.

Paratypes — NMC No. 15615 (3 females) collection data as for Holotype. NMC No. 15614 (4 males) collection data as for Holotype.

Etymology — The species name refers to the province of its type locality.

Description of female (Fig. 1; Fig. 3A–D) — Body stout, somewhat tumefied anteriorly (Fig. 1D, G). Metasome about 3.5 times length of urosome. Total length 2.58–2.84 mm based on 13 specimens. Rostrum absent, but 2 minute sensory hairs present on forehead. Last thoracic segment produced posterolaterally into acute points reaching to about midlength of genital segment; points directed posteriorly. Urosome stout. Genital segment large, almost spherical in appearance. Second and third segments about equal in length. Anal segment shortest. Caudal rami slightly longer than wide, with 4 long terminal setae, 1 short external seta, and 1 short ventral seta.

First antennae (Fig. 1B) 24-segmented, reaching approximately to the anal segment. Some sensory filaments present.

Basipod of second antenna (Fig. 1K) with 4 setae, 2 placed proximally, 2 distally. Exopod 7-segmented, first segment without setae, second segment with 3 setae placed on small protuberances; all other segments of exopod with 1 seta except seventh with 3 terminal setae. Second segment of endopod with 14 setae in groups of 3, 5, and 6.

Mandible (Fig. 1C) with strong masticatory blade. Second basipod with 3 internal setae. First endopodal segment with 2 setae. Distal end of second endopodal segment with 10 setae.

First maxilla (Fig. 1E) with first inner lobe having 7 stout spines, 2 less stout, more plumose proximal spines, and 1 large and 1 small seta. Some minute spinules present on first inner lobe. Second and third inner lobes with 4 setae each, third lobe finely spinulated. First outer lobe with 6 large and 1 small setae. Exopod with 11 setae. Endopod 3-segmented, 5 setae on first segment, 4 on second segment, and 11 on distal segment.

Second maxilla (Fig. 1H) with first 6 lobes having 3 setae each. One seta of triads on second to sixth lobes much smaller than others of triad. First 3 lobes ornamented with fine spinules. Endopod with 4 setae.

Maxilliped (Fig. 1F) with first basal segment massive, length about twice width. Second basal segment slightly longer and more slender, with triangular patch of fine spinules proximally. Setation on first 2 segments as in Fig. 1F. First endopodal segment with 5 setae, remaining endopodal segments each with 4 setae.

First pair of swimming legs (Fig. 3A) with endopod reaching approximately to midlength of second exopodal segment. Endopod with prominent tubercle on external margin. Tubercle with fine spinules on its distal margin. Long hairlike spinules present on both external and internal margin of second basipod. External spine of first exopodal segment smaller than other two external spines, usually directed inward on preserved specimens.

Second swimming legs (Fig. 3B) with long

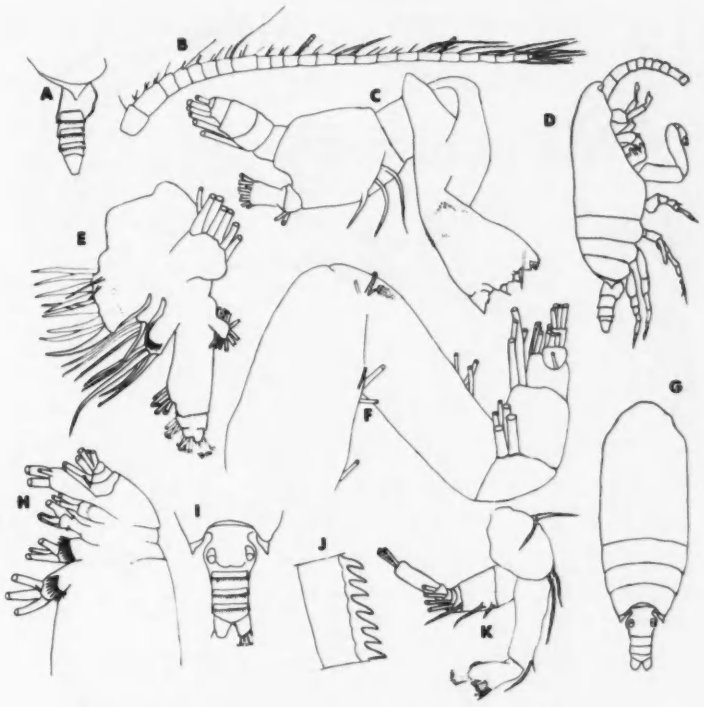

FIG. 1. *Azygokeras columbiae*, n.gen., n.sp. Female: A, posterior part of body, lateral view; B, first antenna; C, mandible; D, habitus, lateral view; E, first maxilla; F, maxilliped; G, habitus, dorsal view; H, second maxilla; I, posterior part of body, dorsal view; J, part of terminal spine on exopod of swimming leg; K, second antenna.

spinules on external margin of first basipod. Three separate rows of spinules run from anterior to posterior surface of basipod on well-preserved specimens. Single row of about 7 shorter, stouter spinules present on second basipod where exopod joins this segment. Posterior surface of endopodal segments ornamented with similar spinules. Last endopodal segment with patch of much smaller and finer spinules at distal end. Exopod without spinulation. External spines large. Terminal spine with about 34 strong teeth not joined by a lamella.

Third pair of swimming legs (Fig. 3C) with spinulation as in second pair.

Fourth swimming legs (Fig. 3D) without spinulation on first and second basipod. Posterior surface of endopods covered with minute spinules similar to those found on the distal part of the last endopodal segment of second and third swimming legs.

Description of male (Fig. 2; Fig. 3E) — General shape of metasome (Fig. 2F, J) quite different in appearance from female. Body not as stout, not tumefied anteriorly. Metasome about 3 times length of urosome. Total length 2.08–2.10 mm based on 3 specimens. Rostrum absent, sensory hairs present on forehead. Last thoracic segment much reduced, less distinguishable than in female. Terminal points also less pronounced but with small dorsally directed spinule terminating each point. Anal segment reduced, other segments approximately equal in length.

Left first antenna 22-jointed (Fig. 2B), right first antenna 21-jointed (Fig. 2A). Eighth and

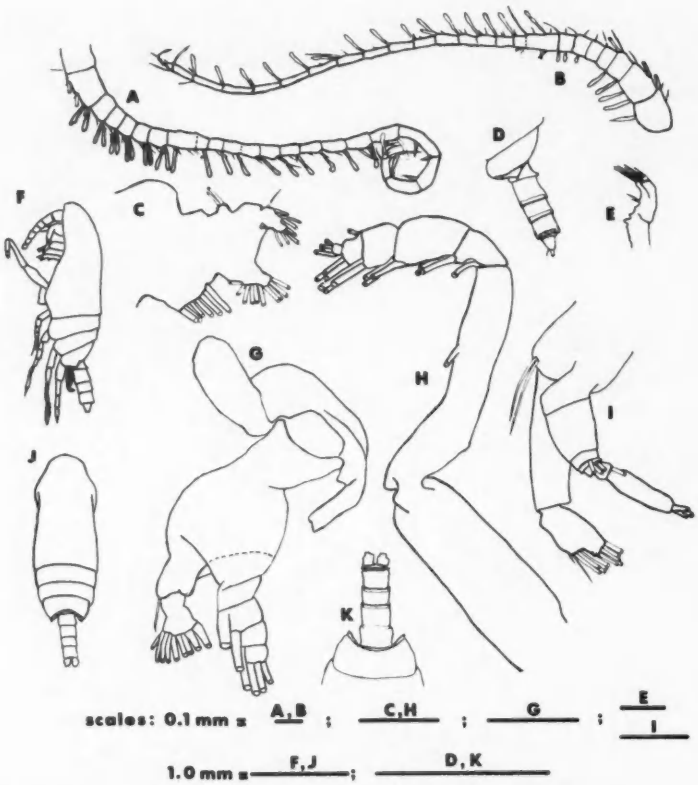

FIG. 2. *A. columbiae*, n.gen., n.sp. Male: A, right first antenna; B, left first antenna; C, first maxilla; D, posterior part of body, lateral view; E, second maxilla; F, habitus, lateral view; G, mandible; H, maxilliped; I, second antenna; J, habitus, dorsal view; K, posterior part of body, dorsal view.

tenth segments of both antennae fused. Eighth segment formed from 3 segments with faint partial suture line between second and third of these segments. Tenth segment formed from 2 segments with partial suture line between them. Aestetes damaged but probably 2 or more present on each proximal segment up to and including eighth. One distal aestete on all other segments. Right first antenna with last 6 segments considerably enlarged. Distal portion bent backward at third and fourth segment from end and curled slightly inward. Each distal seta of terminal segments developed into stout spine with point drawn out into fine hair. Otherwise similar to left first antenna.

Second antennae (Fig. 2I) similar to female except for the following differences in setation: second endopodal segment without setae; terminal segment of exopod with reduced number of setae.

Mouth parts reduced (Fig. 2C, E, G). Mandible without masticatory edge. First maxilla without setae on inner lobes. Second maxilla particularly small, lobes distinguishable, setation reduced.

Maxillipeds (Fig. 2H) more slender than in female. Second basal segment with 1 median seta. First endopodal segment with 4 setae, second and third endopodal segments with 3 setae each, fourth and fifth endopodal segments with 4 setae each.

First pair of swimming legs similar to female with the following exception: long, fine spinules present on external margin of first basipod.

Remaining swimming legs with segmentation and spinulation as in female.

Fifth legs (Fig. 3E) with first basipod of left leg about as long as both basipods of right leg combined. Second basipod of left leg slightly

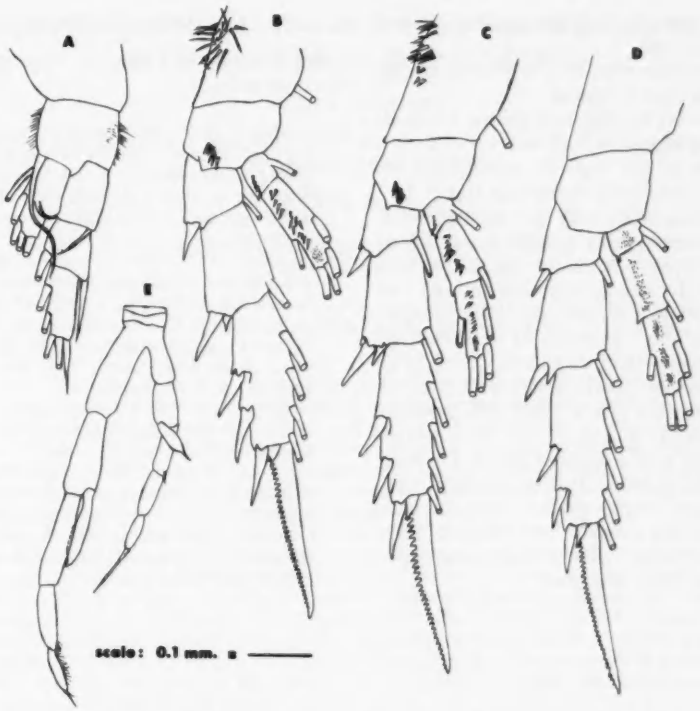

FIG. 3. *A. columbiae*, n.gen., n.sp. Female: A, first swimming leg; B, second swimming leg; C, third swimming leg; D, fourth swimming leg. Male: E, fifth legs.

shorter than first basipod. Exopods of both legs 3-segmented, endopods 1-segmented, more or less rudimentary. Both rami of left leg longer than those of right leg. Right endopod with weak terminal seta. Last segment of left exopod and distal part of second segment with fine spinules on the inner margin. Terminal segment of right exopod with short terminal seta and long slender spine about 1.3 times length of segment.

Discussion

Azygokeras is a typical aetidid agreeing with all characteristics of the family as described by Brodskii (1950) except in the asymmetrical first antennae of the male, and the equal rami of the second antennae. Within the Aetideidae, *Azygokeras* resembles certain genera of larger copepods considered to be epibenthic or planktobenthic. Points of similarity are:

1. First antennae of female with long transversely striated setae as in *Sursamucro*, *Lutamator*, and *Crassantenna*; with these setae particularly numerous distally as in *Bradyidius* and *Pseudoeucheata*.

2. Second antennae with rami equal as in *Pseudoeucheata*, *Sursamucro* and *Lutamator*.

3. Posterior borders of abdominal segments fringed with well-defined teeth or spinules as in *Sursamucro*.

4. Rostrum absent as in *Chiridius*, *Comantenna*, and *Bradyetes*.

5. Endopods of swimming legs with posterior surface spinulated as in *Pseudoeucheata*, *Sursamucro*, and some species of *Bradyidius*.

Major characteristics that distinguish *Azygokeras* from all of the above genera are:

1. Asymmetry of the first antennae of the male. This asymmetry does not involve an articulation as in the Heterarthrandia. The right antenna of *Azygokeras* appears to be used as a grasping organ as evidenced by the enlarged, curled distal

portion, and by the stout spines directed toward the center of the curl.

2. Setation of the first two segments of the exopod of the second antennae.

3. Spinulation on the first and second basipods of the swimming legs.

4. Differences in the type of spinulation between the third and fourth swimming legs.

Azygokeras columbiae may be an epibenthic copepod since almost every specimen was found in the deepest depth interval of the 12 vertical series examined. Its association with the sea bed appears to be relatively loose since the deepest interval sampled only to about 50 m above the bottom. Only two other calanoids, *Bradyidius saanichi* and *Tharybis fultoni*, have been described from British Columbia (Park 1966; 1967) which may be epibenthic. Like *Azygokeras* these species were not collected with a benthic sledge but were apparently caught in deeply hauled plankton nets. The occurrence of these species suggests that collections made from near the bottom with appropriate gear might yield many other epibenthic calanoids from this area.

Acknowledgments

We thank Dr G. Grice for his useful criticism of the manuscript.

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Autotrophic Production in Carnation Creek, a Coastal Rainforest Stream on Vancouver Island, British Columbia

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STOCKNER, J. G., AND K. R. S. SHORTREED. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. J. Fish. Res. Board Can. 33: 1553–1563.

Attached algal growth in Carnation Creek and its estuary were monitored in 1974 and 1975 as part of the Carnation Creek Experimental Watershed Project. Net production on the estuary was 17.8 μg organic matter (org)·cm^{-2}·day^{-1}, and in Carnation Creek the average was 3.4 μg org·cm^{-2}·day^{-1}. Algal growth in Ritherdon Creek, located in an adjacent logged watershed, was slightly higher (4.6 μg org·cm^{-2}·day^{-1}) than the Carnation Creek average. In a streamside nutrient enrichment experiment, nitrate and phosphate concentrations in one trough were increased to twice the normal Carnation Creek values present in the control. In 35 days the nutrient-enriched trough had a total algal volume 3 times that of the control. It is suggested that extremely low nutrient concentrations (especially phosphate), and secondarily, poor light conditions under the canopy, are responsible for the paucity of algal growth in Carnation Creek. Major loss of algae from the system is caused by periodic freshets which scour the stream bed. Losses by grazing herbivorous insects were considered negligible. Dominant diatoms in Carnation Creek were *Achnanthes minutissima*, *Synedra ulna*, *Hannaea arcus*, *Diatoma hiemale*, and *Eunotia pectinalis*. *Ulothrix* sp., *Draparnaldia* sp., and *Mougeotia* sp. were the dominant filamentous green algae. Net production and algal biomass (chlorophyll *a*) in Carnation Creek are among the lowest ever reported in the literature.

STOCKNER, J. G., AND K. R. S. SHORTREED. 1976. Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia. J. Fish. Res. Board Can. 33: 1553–1563.

Nous avons suivi de façon continue la croissance d'algues fixées dans le ruisseau Carnation et son estuaire en 1974 et 1975, comme partie du Projet du bassin expérimental du ruisseau Carnation. La production nette dans l'estuaire est de 17.8 μg de matière organique (org)·cm^{-2}·jour^{-1}, et dans le ruisseau Carnation la moyenne est de 3.4 μg org·cm^{-2}·jour^{-1}. La croissance algale dans le ruisseau Ritherdon, situé dans un bassin avoisinant où se fait le flottage de billots, est légèrement plus élevée (4.6 μg org·cm^{-2}·jour^{-1}) que la moyenne du ruisseau Carnation. Dans une expérience d'enrichissement en substances nutritives sur le bord du cours d'eau, nous avons augmenté dans une auge les concentrations de nitrates et de phosphates à un niveau deux fois plus élevé que le niveau normal du ruisseau Carnation présent dans l'auge témoin. Après 35 jours, l'auge enrichie de substances nutritives a un volume total d'algues 3 fois plus grand que celui de l'auge témoin. Nous suggérons que la pauvreté en algues du ruisseau Carnation est due à des concentrations extrêmement basses de substances nutritives (surtout phosphates), et secondairement à de pauvres conditions d'éclairage sous le canapé. Les crues périodiques qui balayent le lit du cours d'eau sont responsables de la majeure partie de la perte d'algues dans le système. Les pertes causées par les insectes herbivores brouteurs sont considérées comme négligeables. Les diatomées dominantes du ruisseau Carnation sont *Achnanthes minutissima*, *Synedra ulna*, *Hannaea arcus*, *Diatoma hiemale* et *Eunotia pectinalis*. *Ulothrix* sp., *Draparnaldia* sp. et *Mougeotia* sp. sont les algues vertes filamenteuses dominantes. La production nette et la biomasse algale (chlorophylle *a*) du ruisseau Carnation sont parmi les plus faibles jamais signalées dans la littérature.

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STUDIES were initiated in March 1974 to assess attached algal growth and production in Carnation Creek Experimental Watershed, Vancouver Island, B.C. The 1974 program was the 5th consecutive yr of intensive prelogging data collection on Carnation Creek, and the last year the watershed remained undisturbed. The overall objectives of the Carnation Creek Project are: a) to develop a better understanding of how undisturbed coastal rainforest–salmonid stream ecosystems work in order; b) to explain and quantity the impacts of timber production activities on stream environments and their capacity to produce salmonid fishes in sufficient detail; and c) to provide continuous input to the further development of integrated resource management guidelines (Narver 1974).

Within the scope of these broad objectives was the assessment of prelogging autotrophic stream production including an appraisal of factors known to influence attached algal growth and distribution in these ecosystems.

Description of Study Area

Carnation Creek flows into Barkley Sound on the west coast of Vancouver Island, B.C. The watershed is in the western hemlock biogeoclimatic subzone with a very high annual rainfall of 2.8–3.6 m (Fig. 1). Stream flow is highly variable, ranging from .025 in summer to 39 $m^3 s^{-1}$ during winter freshet. The stream supports small populations of resident cutthroat trout (*Salmo clarki*) in its upper reaches, and is accessible for only 3 km to anadromous fish, namely chum salmon (*Onchorhynchus keta*), coho salmon (*O. kisutch*), and steelhead trout (*S. gairdneri*). The watershed area is approximately 10 km^2, and contains no lakes.

Methods

The extreme ranges of flow common in Carnation Creek necessitated use of samplers capable of withstanding considerable variation in flow velocity. Concrete blocks 31 × 31 × 18 cm with two threaded steel pins embedded in their upper surfaces were constructed (Fig. 2A). Each block weighed between 45 and 50 kg. Plates of 1-cm thick plexiglass were bolted to the pins, 5–7 cm above the surface of the block. The upper surfaces of the plexiglass plates were roughened with fine steel wool and divided into four 100-cm^2 quadrants (Fig. 2B).

Six samplers were placed in Carnation Creek in a variety of habitats within predefined study areas (Table 1). Two were placed in Ritherdon Creek in an adjacent watershed that was clear-cut logged and burned to the stream edge in 1969. Remaining samplers (two in 1974 and four in 1975) were placed at various tidal heights on the Carnation Creek estuary (Table 1; Fig. 1). At each station the sampler was embedded in gravel to a depth of about

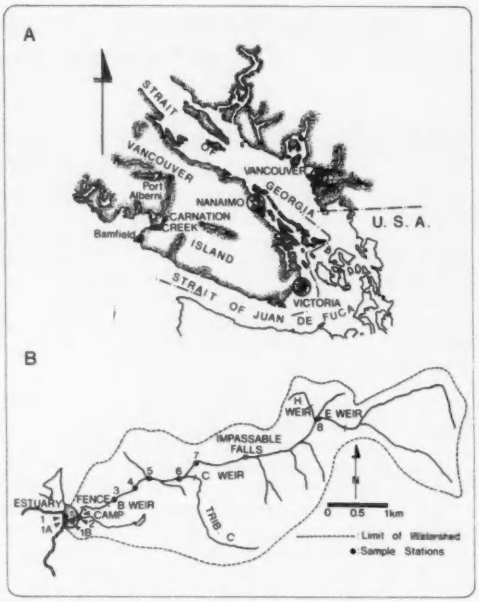

FIG. 1. Southern portion of Vancouver Island showing location of Carnation Creek, and detailed map of Carnation Creek watershed with station locations.

18 cm. The corner of the block was placed perpendicular to the direction of streamflow to reduce resistance and ensure a more even flow over the plexiglass plate.

In 1974 sampling intervals varied from 2 wk at times of high production (good light, low flow), to 4 wk during periods of low production (high flow and/or low light). In 1975 samples were obtained at monthly intervals. It was initially assumed and later verified, that time between sampling periods (3–4 wk) was of sufficient duration to enable a relatively stable population to develop.

Sampling consisted of removing the plexiglass plate from the block, scraping the accumulated growth from each quadrant into a glass jar, and immediately returning the cleaned plexiglass plate to the block. The most efficient scraper was a clean glass microscope slide.

The contents of one jar were filtered onto a 5.5-cm Whatman glass fiber filter. One milliliter of saturated $MgCO_3$ solution was added to prevent acidification prior to analysis. Filters were folded, placed in aluminum weighing dishes, and frozen. Chlorophyll was extracted using methods of Yentsch and Menzel (1963), with minor modifications used when algal growth was exceptionally heavy. Filters were macerated in a tissue grinder with 10 ml of 90% acetone, and the filtrate was analyzed for chlorophyll *a* on a Cary (Model 15) recording

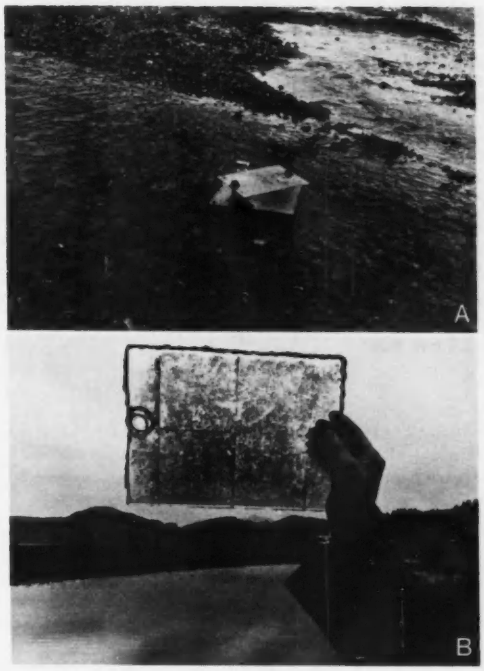

FIG. 2. A, Sampler with plexiglass plate attached; B, Plexiglass plate prior to sampling after 4-wk growth.

spectrophotometer. The equation of Strickland and Parsons (1968) was used to calculate chlorophyll *a*.

The contents of one jar were filtered onto an ashed and weighed 5.5-cm Whatman glass fiber filter. Filters were folded, placed in aluminum weighing dishes, and frozen. Samples were dried at 105 C to constant weight, weighed, ashed at 500 C for 4 h in a muffle furnace, and weighed again. Values are expressed as ash-free dry weight (organic = loss-on-ignition) cm^{-2}.

Net production (accumulation) was estimated by dividing total organic accumulation over a given sampling interval by the number of days in the interval. Values are expressed as micrograms organic matter cm^{-2} day^{-1}. For purposes of comparison with literature values, carbon was estimated as 50% of organic (loss on ignition) weight (Stockner and Armstrong 1971).

Lugol's acetate solution was added to two of the jars. A portion of the algae from one jar was counted using a Zeiss inverted plankton microscope (160 and 470×). This count determined relative abundance of major algal groups and identified nondiatom algae to the genus level.

Permanent quantitative Hyrax mounts of diatoms were made from one 100-cm^2 quadrat. Counts from these slides were converted to number of diatoms·cm^{-2} using methods described by Stockner and Armstrong (1971). The abundance of diatoms relative to other algal groups, calculated from inverted microscope counts, was applied to this value to give total algal cells·cm^{-2}. Algal volumes were determined using values calculated by Nauwerck (1963), and by Evans and Stockner (1972), although some direct volume estimates were made by the authors.

The relative abundance of each diatom species was calculated and used in a "distance" index (MacIntosh 1967), to compare similarities between diatom communities in the stream.

Light to the canopy (overstory) was measured using a Belfort recording pyrheliometer placed on a clear-cut-logged hill beside the Carnation Creek estuary. A second pyrheliometer was placed for 2 wk beside the first (for calibration), and then for 2-wk intervals beside each stream sampler under the forest canopy and in Ritherdon. Using these data, percentage of total available light reaching the samplers was calculated for each sampling interval (Table 1).

Current velocity was measured at only one level of flow (0.23 $m^3 \cdot s^{-1}$) by recording the average time taken for a small stick to travel 1 m. Temperature was recorded on a Lambrecht distance thermograph (Model 256).

Nutrient concentrations, major ions, and stream discharge were monitored throughout the study using methods and instrumentation described by Scrivener (1975).

In August and September 1975 a streamside nutrient enrichment experiment was conducted in Carnation Creek. Creek water from B weir (Fig. 1), was piped into a header-box, split equally into two chambers, and discharged onto two identical troughs 3.5 m long × 15 cm wide, with 5-cm sides). A concentrated solution of $NaNO_3$ and Na_2HPO_4 in an N:P ratio of 11:1 was dripped into one chamber of the header-box to produce concentrations in one trough approximately double mean nitrate and phosphate concentrations in natural Carnation Creek water.

Prior to any nutrient additions, each trough had 4 wk to establish an attached algal community. Sampling consisted of removing all accumulated growth from a known area (usually 100 cm^2) on each trough at weekly intervals. Each sample came from upper undisturbed portions of each trough. Each sample was split into four equal portions which were used for determination of chlorophyll *a*, ash-free dry weight, and algal numbers, volume, and species composition.

Results

Percentage of total available light that actually reached the samplers in Carnation Creek ranged from 5% at Station 8, with heavy canopy and understory, to 47% at Station 3, with moderate canopy openings and little overhanging streamside vegetation (Table 1). Stations 4, 5, 6, and 7 had similar light conditions with reductions by

TABLE 1. Salient information on station locations in Carnation and Ritherdon creeks, 1974 and 1975.

Station no.	Location	Description	Current velocity cm · s^{-1} (at low flow)	% available light
		Estuary		
1	extreme edge of estuarine fan	predominantly marine 10 m from creek channel exposed on a 0.8-m tide	—	100
1A	extreme edge of estuarine fan	predominantly marine in creek channel exposed on a 0.6-m tide	—	100
1B	100 m from edge of fan	brackish	—[a]	100
2	edge of forest canopy	brackish	—[a]	65
		Carnation		
3	630 m	pool	9	47
4	1150 m	run	24	39
5	1480 m	pool	11	37
6	2000 m	riffle	64	42
7	2350 m	run	36	36
8	4500 m	pool	4	5
		Ritherdon		
9		riffle	56	72
10		pool	20	72

[a]Current flow variable, dependent on tide level.

forest canopy of 40, 39, 40, and 36%, respectively. Stations on the estuary received full sunlight, while Station 2, on the edge of the estuary was beneath streamside vegetation and received only 65% of available light. Both stations in clear-cut-logged Ritherdon Creek received 72% of total available light.

Late fall, winter, and early spring discharges in Carnation Creek were extremely variable, with an annual mean of 1.56 $m^3 \cdot s^{-1}$ (Fig. 3). Station 1 on the estuary fan was away from any direct current influence, but was subject to considerable wave action. Flow velocity over Stations 1B and 2 was dependent upon tidal height, but never exceeded 35 cm s^{-1}. Velocity of flow over samplers in Carnation ranged from 4 cm s^{-1} at Station 8 to 64 cm s^{-1} at Station 6 (Table 1).

An arbitrary classification of current velocities into pool (0–20 cm s^{-1}), run (21–45 cm s^{-1}), and riffle (46–100 cm s^{-1}) was made. Stations 3, 5, and 8 were located in pools, Station 4 and 7 in runs, and Station 6 in a riffle. Stations 9 and 10 in Ritherdon Creek were in riffle and pool, respectively (Table 1). This classification is probably an accurate representation of conditions during summer low-flows, but not during most winter flows or sudden freshet periods.

Water temperature at B weir (Fig. 1) ranged from lows of 2.0 C in January to highs of 12 C in August in both years (Fig. 3). Diurnal stream temperature variation did not exceed 2.5 C. Temperatures in Ritherdon Creek ranged from winter lows of 2.0 C to summer highs of 18 C. Diurnal variation in Ritherdon was up to 4.0 C in summer.

Water temperatures on the estuary were subject to greater seasonal and diurnal variation because of tidal conditions, variable stream flow, and more open exposure to direct sunlight.

Dominant major ions in Carnation are calcium, sodium, bicarbonate, chloride, silicate, and sulfate, with only trace amounts of iron, manganese, potassium, and magnesium (Scrivener 1975). The extremely low total dissolved solids value in both Carnation and Ritherdon creeks is indicative of the oligotrophic nature of surface water discharges from both watersheds (Table 2).

Nutrient concentrations in both Carnation and Ritherdon creeks are very low, with silicate the most abundant nutrient (Table 2). Almost all of

TABLE 2. Water chemistry, Carnation and Ritherdon creeks.

	Mean values Carnation July 1971–May 1974[a]	Mean values Carnation from six dates in 1975[b]	Mean values Ritherdon from same six dates in 1975[b]
Major ions ($mg \cdot liter^{-1}$)			
Ca^{2+}	3.0	2.6	4.3
Mg^{2+}	0.5	0.6	0.6
Na^{+}	2.0	2.3	1.9
K^{+}	0.1	0.2	0.4
Cl^{-}	2.4	3.1	3.4
Fe^{3+}	0.04	0.01	0.04
Mn^{2+}	<0.01	<0.01	<0.01
SO_4^{2+}	3.7	3.2	4.7
HCO_3^{-}	8.4	—	—
Nutrients ($\mu g \cdot atoms \cdot liter^{-1}$)			
NO_3^{-}(N)	2.50	3.13	7.89
NH_4^{+}(N)	0.30	0.40	0.40
TP	0.05	0.09	0.11
SiO_2	34.0	24.8	24.2
TDS ($mg \cdot liter^{-1}$)	25.0	27.8	36.3

[a]After Scrivener (1975).
[b]J. C. Scrivener unpublished data.

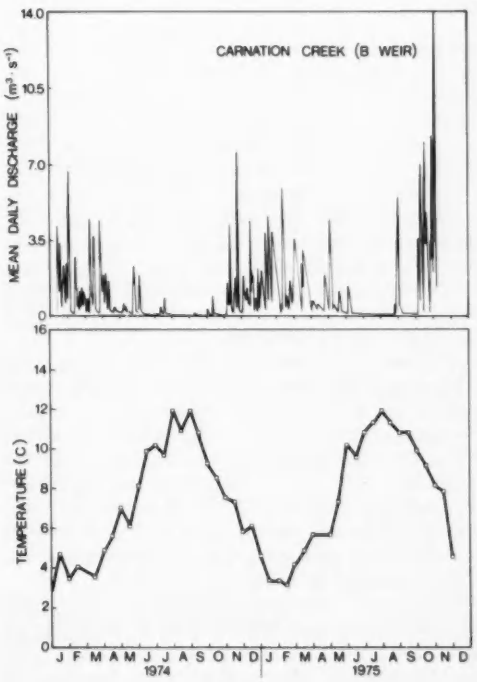

FIG. 3. Mean daily discharge and temperature at B weir, in Carnation Creek, 1974 and 1975.

the total phosphorus measured was dissolved orthophosphate with a mean concentration of 0.05 μg atoms liter^{-1}, ranging from <0.01 to 0.29 μg atoms liter^{-1}. The mean nitrate concentration was 2.5 μg atoms liter^{-1}, with concentrations varying from lows of 0.5 to highs of >6.0 μg atoms liter^{-1}. With the exception of some freshet periods, nitrate and silicate concentrations showed a significant inverse relation with discharge (Scrivener 1975). Ritherdon Creek displayed slightly higher values of most dissolved constituents than Carnation (Table 2).

Mean chlorophyll *a* concentrations for both years in Carnation Creek estuary were nearly an order of magnitude greater than either Carnation or Ritherdon creeks (Table 3). Lowest mean concentrations were at Station 8, under heavy forest canopy, 0.21 $\mu g \cdot cm^{-2}$, and highest at Station 1A on the estuary, 3.99 $\mu g \cdot cm^{-2}$. Mean values for Carnation Creek were slightly lower than Ritherdon Creek values for both years.

Seasonally, greatest concentrations on the estuary and in Carnation occurred during an exceptionally warm, dry fall in 1974, while in Ritherdon Creek concentrations were highest in May and June of 1974 (Fig. 4). In 1975 the estuary showed peak values from February to April, while Carnation and Ritherdon creeks displayed little seasonal variation.

Mean ash-free dry weight value on the estuary

TABLE 3. Mean values of attached algal biomass, net production, and percentage diatoms at 10 stations in study area in 1974 and 1975. Grand means for estuary (Stations 1, 1A, 1B, 2), Carnation Creek (Stations 3–8), and Ritherdon Creek (Stations 9 and 10) listed below station means.

Station	Chloro-phyll *a* ($\mu g \cdot cm^{-2}$)	Ash-free dry wt ($\mu g \cdot cm^{-2}$)	Algal cells ($no. \cdot cm^{-2}$)	Diatoms ($no. \cdot cm^{-2}$)	Algal vol ($mm^3 \cdot cm^{-2}$)	% of Diatoms in Total vol	Net production ($\mu g\ org \cdot cm^{-2}\ day^{-1}$)
1	1.73	805	2.23×10^{6}	1.62×10^{6}	1.53	92	30.9
1A[a]	3.99	635	1.25×10^{6}	9.89×10^{5}	0.88	90	18.8
1B[b]	0.46	344	2.18×10^{6}	1.16×10^{6}	0.54	86	10.8
2	1.26	302	3.04×10^{6}	1.48×10^{6}	0.96	66	10.7
3	0.19	110	1.28×10^{6}	2.20×10^{5}	6.93×10^{-2}	54	4.2
4	0.12	100	8.13×10^{5}	1.85×10^{5}	5.45×10^{-2}	70	3.9
5	0.19	144	1.01×10^{6}	2.79×10^{5}	6.16×10^{-2}	52	5.5
6	0.12	38	4.55×10^{5}	7.80×10^{4}	3.19×10^{-2}	56	1.6
7	0.21	86	9.56×10^{5}	2.11×10^{5}	7.53×10^{-2}	52	3.5
8	0.09	43	1.10×10^{5}	2.41×10^{4}	6.55×10^{-3}	68	1.6
9	0.19	98	6.55×10^{5}	3.54×10^{5}	2.26×10^{-1}	78	4.0
10	0.26	138	7.34×10^{5}	3.68×10^{5}	9.83×10^{-2}	69	5.2
				Grand means			
1[b]	1.72	533	2.52×10^{6}	1.49×10^{6}	1.18	82	17.8
2	0.16	87	8.02×10^{5}	1.66×10^{5}	4.99×10^{-2}	60	3.4
3	0.23	118	6.95×10^{5}	3.61×10^{5}	1.62×10^{-1}	74	4.6

[a]1975 only.
[b]1, Carnation Creek estuary; 2, Carnation Creek; 3, Ritherdon Creek.

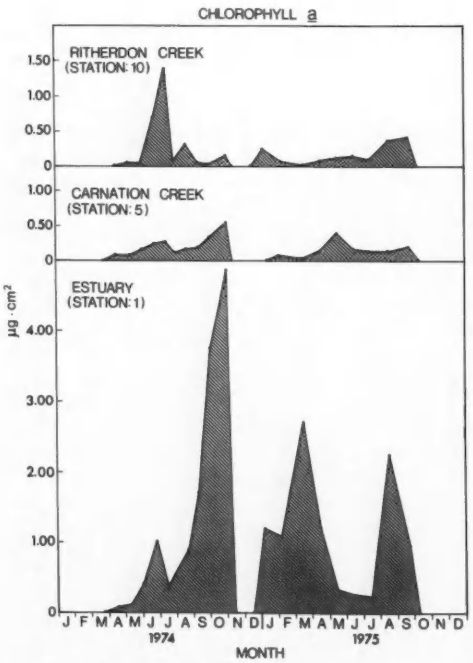

FIG. 4. Seasonal variation in chlorophyll *a* concentration at Stations 1, 5, and 10 in estuary, Carnation Creek, and Ritherdon Creek, respectively.

for both years was 533 μg org·cm^{-2}, which was over 6 times the Carnation Creek values, and 5 times the Ritherdon Creek value (Table 3). Highest values were at Station 1 on the estuary, and lowest at Station 8 under heavy forest canopy (Table 3). Seasonal variation was similar to that discussed for chlorophyll *a* (Fig. 4).

Diatoms were the dominant algal group by volume in all habitats in Carnation and Ritherdon creeks. *Achnanthes minutissima* was the dominant species at all stations except on the estuary, where a more diverse diatom assemblage occurred, with no single species dominant.

The most common diatoms on the estuary were *Cocconeis* spp., *Licmophora* spp., *Nitzschia* spp., *Navicula* spp., and *Synedra tabulata*. Diatoms occurring commonly in Carnation Creek were *Diatoma hiemale*, *Fragilaria* sp., *Eunotia pectinalis*, *E. tenella*, *Gomphonema parvulum*, *S. ulna*, and *Tabellaria flocculosa*. *Synedra ulna* and *D. elongatum* were more abundant in Ritherdon than in Carnation Creek. A complete species list is presented in Table 4.

The most common nondiatom algae were *Microcystis* sp. and an unidentified flagellate in a gelatinous matrix closely resembling *Chromulina* sp. Filamentous chlorophytes such as *Draparnaldia* sp., *Mougeotia* sp., and *Ulothrix* sp. were more prevalent in Ritherdon than Carnation, at times forming a mat covering large areas of creek

TABLE 4. Species list and computed volumes of attached algae in Carnation Creek, Ritherdon Creek, and Carnation Creek estuary (Volume computed for dominants only).

Diatoms	Vol (μ^3)
Carnation and Ritherdon creeks	
Achnanthes lanceolata (Breb). Grun.	50
A. minutissima Kutz	30
Achnanthes sp.	20
Capartogramma crucicula (Grun. ex Cl.) Ross	—
Cocconeis placentula Ehr.	240
Cymbella turgida (Gregory) Cleve.	200
C. ventricosa Kutz	2500
Cybella sp.	500
Diatoma heimale (Roth) Heib.	450
D. elongatum (Lyngb.) Ag	250
Eunotia diodon Ehr.	—
E. lunaris (Ehr.) Grun.	1500
E. pectinalis (Kutz.) Rabh.	700
E. perpusilla Grun.	300
E. sudetica O. Mull.	200
E. tenella (Greve) Cleve	50
Fragilaria sp.	100
Frustulia rhomboides var. saxonica (Rabh.) Det.	3000
F. rhomboides var. capitata (A. Mayer) Patr.	2000
Gomphonema constrictum (Ehr.) V.H.	1000
G. lanceolatum Ehr.	2000
G. parvulum Kutz	300
Hannaea arcus (Ehr.) Patr.	500
Meridion circulare var. constrictum (Ralfs) V.H.	200
Navicula sp.	400
Nitzschia sp. A	800
Nitzschia sp. B	50
Stauroneis phoenicenteron (Nitz.) Ehr.	—
Stauroneis sp.	—
Synedra ulna (Nitz.) Ehr.	3300
Synedra sp.	—
Tabellaria fenestrata (Lyngb.) Kutz.	3000
T. flocculosa (Roth.) Kutz.	1000
Nondiatom algae	
Batrachospermum sp.	—
Draparnaldia sp.	—
Microcystis sp.	20
Mougeotia sp.	200
Oscillatoria sp.	4
Rhizoclonium sp.	—
Spirogyra sp.	—
Ulothrix sp.	170
Zygnema sp.	—
Unidentified colonial flagellate	50
Diatoms	
Carnation Creek Estuary	
Achnanthes brevipes Agardh.	1000
Amphiprora surrirelloides Hendey	—
Amphora sp.	—
Biddulpjia laevis Ehr.	—
Caloneis sp.	—
Cocconeis placentula var. lineata (Ehr.) V.H.	240
Cocconeis sp.	—
Coscinodiscus radiatus Ehr.	—
Diploneis sp.	—
Grammatophora serpentina Ehr.	600
Licmophora gracilis (Ehr.) Grun.	7000
Melosira juergensii Agardh	4000
M. nummuloides Agardh	7000
Navicula inflexa	50
N. clementis	50
Navicula sp.	—
Nitzschia bilobata Wm. Smith	1000
Pleurosigma elongatum Wm. Smith	—
Rhiocosphenia sp.	—
Surirella ovata Kutz	1500
Synedra pulchella Kutz	2000
S. tabulata (Agardh.) Kutz	3000
Nondiatom algae	
Enteromorpha sp.	—
Fucus sp.	—
Pylaiella sp.	—
Ulothrix sp.	170

bed. The rhodophyte *Batrachospermum* sp. was observed at irregular intervals in both Carnation and Ritherdon creeks. *Ulothrix* sp. was common in early spring and late fall, but was rarely observed in summer months. A detailed discussion of algal succession and species composition appears in Stockner and Shortreed (1975).

The greatest volume of algae occurred on the estuary, where the mean for both years was 1.18 $mm^3 \cdot cm^{-2}$. Ritherdon Creek had a slightly higher mean algal volume than Carnation (Table 3).

The percentage of total algal volume contributed by diatoms varies seasonally (Stockner and Shortreed 1975). Diatoms were least important early in the year, increasing steadily to gain dominance at most stations during low-flow periods.

There was nearly an order of magnitude difference in mean algal density for both years between Carnation estuary and Creek stations (Table 3). The mean value for Ritherdon was twice the Carnation Creek value. There was no well-defined period of maximum algal abundance (Stockner and Shortreed 1975).

Greatest growth was noted on the estuary, notably in September 1974, and in March and August 1975 (Table 3; Fig. 4). Algal growth rates in Carnation and Ritherdon creeks were much lower than those seen on the estuary and showed no clear seasonal maxima.

Stations 3, 4, and 5 in Carnation Creek were most similar to one another, with mean values

of D_{jh} for both years ranging from 16 to 22 (Table 5). Stations on the estuary showed a greater similarity to one another than to any other stations in Carnation or Ritherdon creeks. Station 10 in Ritherdon was most similar to Stations 3, 4, and 5 in Carnation Creek (Table 5).

There was a marked difference between algal growth in the control and enriched troughs (Fig. 5). After 35 days there were 3 times as many diatoms, 3 times the total algal volume, and over twice the amount of chlorophyll and organic matter·cm^{-2} on the nutrient-enriched trough than on the control trough. The nitrogen and phosphorus content in the enriched side was always double the Carnation Creek values, and differences in nitrate values between enriched and control troughs showed greater variation than did phosphate (Fig. 5A).

Discussion

If light were the major factor limiting algal growth then removal of the forest canopy would result in an immediate increase in production. This has happened only to a limited extent in Ritherdon Creek, on the adjacent clear-cut-logged watershed, which suggests that factors other than light may be limiting algal growth in these streams. Nonetheless, the importance of light to algal growth in Carnation Creek and estuary is demonstrated by the significant, positive relation between mean chlorophyll *a* (biomass) and percent light reduction by forest canopy at each station for both years (Fig. 6).

Values from Carnation Creek Stations 3–8 are clustered near the ordinate and represent a low light–low chlorophyll condition. Values from the estuary are separated from the other and represent a high light–high chlorophyll, as well as high nutrient situation. When Ritherdon Creek values are plotted (Fig. 6), the relation is no longer significant. This is because it is likely that nutrients, not light, prevent greater growth in Ritherdon, and produce the observed high light–low chlorophyll condition.

Another interesting observation was the relation between available light and contribution of diatoms to total algal volume (Fig. 7). These data suggest that diatoms, as a group, are better adapted to a moderate to high light situation, than to poor, diffuse light conditions under the canopy.

We consider nutrients the major factor regulating attached algal growth in both Carnation and Ritherdon creeks. Nutrient content of both systems is remarkably low; in fact, all dissolved constituents are present at extremely low levels (Table 2). Greatest algal growth occurred on the Carnation Creek estuary, an area which receives,

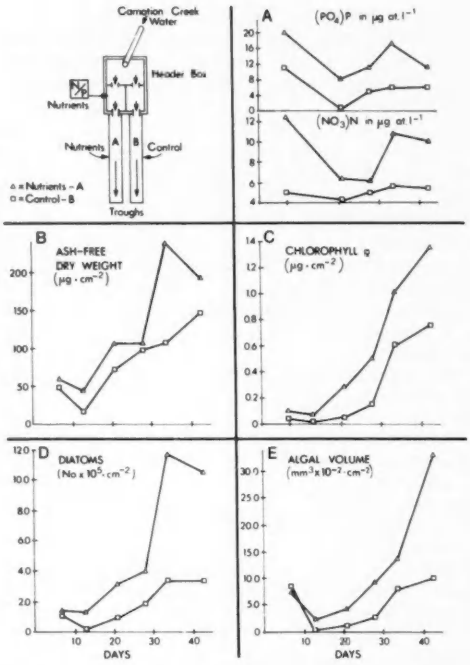

FIG. 5. Nutrient enrichment experiment: diagram of apparatus used and plots of A, nutrient concentrations; B, ash-free dry weight; C, chlorophyll *a*; D, number of diatoms; E, and algal volume; for both experimental and control troughs.

Table 5 set up as an illustration.

Table 5. Matrix of 1974–75 mean distance index[a] (D_{jh}) values for Carnation and Ritherdon creeks.

$$D_{jh} = \sqrt{\sum_{i=1}^{s} \left(x_{ij} - x_{ih}\right)^2}$$

Distance Index

where: D_{jh} = degree of difference between the j^{th} and h^{th} community x_i

x_{ij} = % abundance of i^{th} taxonomy in the j^{th} community

s = number of taxa.

STATIONS	1	1A	1B	2	3	4	5	6	7	8	9
1A	49										
1B	63	63									
2	68	62	70								
3	90	96	96	61							
4	92	97	82	63	21						
5	90	94	95	60	16	22					
6	79	80	87	56	62	44	62				
7	87	89	94	60	30	35	33	48			
8	87	88	79	63	52	40	50	52	46		
9	86	65	81	65	73	62	70	72	78	76	
10	98	99	100	67	24	25	22	63	31	48	50

STATIONS

[a] MacIntosh (1968).

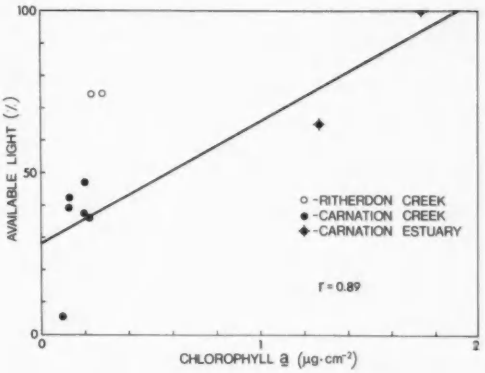

FIG. 6. Linear regression of mean chlorophyll *a* concentration for both 1974 and 1975 and percentage light penetration through the canopy for both years. Ritherdon values not included in regression.

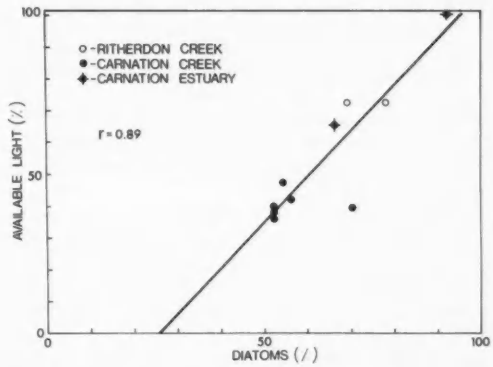

FIG. 7. Linear regression of percentage diatoms of total algal volume and percentage light penetration through the canopy for both years.

in addition to plentiful light, an abundant supply of nutrients from sea water. In Carnation Creek it is likely that phosphate and low light limit growth at all stations, while in Ritherdon phosphate alone limits growth.

The nutrient enrichment experiment demonstrated the response of attached algae to increased nitrate and phosphate concentrations under normal light conditions beneath the forest canopy (Fig. 5). Each nutrient was not tested separately so that relative importance of each cannot be separated at this time. However, because phosphorus is at or near the detection limit throughout much of the year, while nitrate values remain considerably higher, we consider phosphorus concentrations more critical than nitrate in both streams.

There was little diurnal or seasonal variation in water temperature in Carnation and though Ritherdon showed greater variations, annual mean temperatures of both streams were similar. It is unlikely that temperature plays a significant role in limiting production in either stream.

Export of particulate matter in Carnation Creek increases as a linear function of flow, but most of the material is allochthonous (P. Neaves unpublished data). Accumulations of algae on substrates are susceptible to export when flow increases suddenly (freshet). However, Carnation and Ritherdon creeks are so unproductive that in spring and summer visible accumulations of algae are difficult to perceive with the naked eye. Though some losses occur during infrequent freshets in May and June, we suspect that during the growing season (April–October) flows are so low (average 0.23 $m^3 \cdot s^{-1}$) that losses by physical means are negligible.

We made no direct quantitative assessment of grazing rates by streams invertebrates, but did note the direct utilization of attached algae by several species, notably the stonefly *Alloperla severa* and the mayflies *Cinygmula* sp. and *Baetis* sp. From numerous in situ observations and stomach content analysis, grazing losses are apparently not substantial, and account at most for a 5–10% loss of attached algae over a given sampling interval.

If growth in both streams were more rapid and biomass greater, competition for stable substratum could play some role in limiting populations of certain species. However, we feel nutrients and light prevent algal populations from reaching a density where space limitation becomes a problem.

There are few comparable data on Pacific rainforest streams for meaningful comparison of algal communities. Many of the dominants in Carnation or Ritherdon creeks, namely *Achnanthes minutissima*, *Synedra ulna*, and *Diatoma spp.* are also abundant in streams of the Alsea watershed on the Oregon coast (Hansmann 1969). However, there is little similarity in species composition of Carnation and Ritherdon creeks and the flora of artificial streams in Oregon studied by McIntire and Phinney (1965).

Some species displayed rather clear habitat preferences in Carnation and Ritherdon. *Achnanthes minutissima* and *D. heimale* were common in all locations in Carnation under the canopy, except in riffles, where *Hannaea arcus* was dominant. *Diatoma elongatum*, *S. ulna*, and *Tabellaria flocculosa* were more common in Ritherdon than in Carnation suggesting a preference for high

TABLE 6. Comparison of chlorophyll *a* and net production accumulation of attached algal communities, and average nutrient content of water from a variety of habitats.

Community	Chlorophyll *a* (*mg Chlorophyll* $a \cdot m^{-2}$)	Net production ($mgC \cdot m^{-2} \cdot day^{-1}$)	Nutrients ($\mu g\ atoms \cdot liter^{-1}$)	
			$(NO_3)N$	$(PO_4)P$
Carnation Creek	1.6	20	2.5	.05
Ritherdon Creek	2.3	30	5.2	.03
Carnation Estuary	10.7	120	7.0	.70
ALSEA streams, Oregon natural substrate (Hansmann 1969)	60	380–580	13.8	.41
Laboratory Streams, Oregon				
Light adapted	480–2010	1200–3000	4.8	.31
Shade adapted (McIntire and Phinney 1965)	140–1300	800–1900	4.8	.31
Logan River, Utah (McConnell and Sigler 1959)	300–1420	2000–8000	16.1	2.08
Silver Springs, Florida (Odum 1957)	2950	10000	7.4	.20

light conditions. In ultraoligotrophic lakes, diatoms tend to be less numerous than small motile chrysophytes and dinoflagellates (Schindler and Holmgren 1971). In Carnation Creek, although diatoms were common, there was a greater number of algae from other groups, namely chlorophytes and chrysophytes. In Ritherdon Creek and on the Carnation estuary, diatoms were the dominant group throughout the year. In both lenthic and lotic aquatic habitats, poor nutrient conditions tend to reduce the importance of diatoms relative to other algal groups.

The composition of algal communities on the Carnation estuary went from strictly marine species (Station 1) to a community composed of species known to be tolerant to brackish water e.g. *Melosira nummuloides*, *S. tabulata*, and *Surirella ovata* (Pomeroy 1974).

Average values of chlorophyll *a*, net production, and water nutrient content from Carnation Creek and estuary and Ritherdon Creek were among the lowest recorded in the literature (Table 6). In a comparative evaluation of chlorophyll *a* content of attached algae from a variety of habitats by Moss (1968) and Odum et al. (1958), values for Carnation and Ritherdon creeks were lower than attached algal communities growing on arctic sea ice (10–12 $mg \cdot m^{-2}$) (Appolonio 1965, as cited by Moss 1968) Among the highest chlorophyll *a* and production values were from Silver Springs, Florida (Table 6).

Values from the Alsea watershed in western Oregon were considerably higher, likely because of the higher nutrient content of these streams (Table 6). The upper threshold of autotrophic production in flowing waters occurs in tepid springs with abundant nutrients and light, while the lower limit occurs in the nutrient poor conditions typified by Carnation and Ritherdon creeks.

Other evidence of the oligotrophic nature of Carnation Creek can be seen in fisheries and stream benthos data. Juvenile coho salmon normally spend a year in the native stream prior to seaward migration, but in Carnation Creek about 50% require 2 yr to reach sufficient size to migrate (Narver and Anderson 1974). The stoneflies *Alloperla* sp. and *Capnia* sp. have a 1-yr life cycle in most British Columbia streams, but in Carnation Creek have a 2-yr cycle (J. C. Scrivener unpublished data). These observations substantiate our conclusions on autotrophic production and collectively provide sufficient evidence to indicate that these ecosystems are among the least productive ever studied at temperate latitudes.

Acknowledgments

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A Natural Epizootic of Infectious Hematopoietic Necrosis in Fry of Sockeye Salmon (*Oncorhynchus nerka*) at Chilko Lake, British Columbia

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WILLIAMS, I. V., AND D. F. AMEND. 1976. A natural epizootic of infectious hematopoietic necrosis in fry of sockeye salmon (*Oncorhynchus nerka*) at Chilko Lake, British Columbia. J. Fish. Res. Board Can. 33: 1564–1567.

The first confirmed epizootic of infectious hematopoietic necrosis virus disease under natural conditions is reported for sockeye salmon, *Oncorhynchus nerka*, in Chilko Lake, British Columbia. The outbreak occurred among fish of the 1972 brood during the spring of 1973. An estimated 825.6 million eggs were deposited in the Chilko River in 1972, and the production of 31.4 million fry that migrated into the lake in 1973 was significantly lower than the 55.1 million fry expected. The egg-to-fry survival of 3.8% was the lowest ever recorded at Chilko Lake (1949–73). The estimated fry-to-smolt survival of 57.1%, however, was well within the normal range for this lake. Apparently IHN severely reduced the survival of the 1972 brood of sockeye salmon fry at Chilko Lake, and all or nearly all of the reduction occurred during the egg-to-fry stage of the life cycle.

WILLIAMS, I. V., AND D. F. AMEND. 1976. A natural epizootic of infectious hematopoietic necrosis in fry of sockeye salmon (*Oncorhynchus nerka*) at Chilko Lake, British Columbia. J. Fish. Res. Board Can. 33: 1564–1567.

Nous signalons la première épizootie vérifiée de la maladie à virus de la nécrose hématopoïétique infectieuse dans des conditions naturelles chez le saumon nerka, *Oncorhynchus nerka*, du lac Chilko, Colombie-Britannique. L'épidémie apparut chez des poissons de la classe de 1972 au printemps 1973. Environ 825.6 millions d'œufs ont été placés dans la rivière Chilko en 1972, et la production de 31.4 millions d'alevins qui émigrèrent dans le lac en 1973 fut significativement plus basse que les 55.1 millions d'alevins anticipés. La survie de l'œuf à l'alevin de 3.8% est la plus faible jamais enrégistrée au lac Chilko (1949–73). Par ailleurs, la survie estimée de l'alevin au smolt, 57.1%, se situe dans la gamme normale pour ce lac. Il semble que la NHI ait sérieusement réduit la survie de la classe d'alevins de saumon nerka de 1972 au lac Chilko, et que toute ou presque toute la diminution se soit produite au stade d'œuf à alevin du cycle biologique.

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JUVENILE sockeye salmon (*Oncorhynchus nerka*) suffered heavy mortalities at five hatcheries in the State of Washington during the early 1950s (Watson et al. 1954) and in several State of Oregon hatcheries (Parisot et al. 1965). At all these hatcheries the mortality was attributed to what is now known as infectious hematopoietic necrosis (IHN), a viral disease (Wolf 1972; Amend et al. 1973; Amend 1974). Although the disease has been reported as a problem only in fish hatcheries, the IHN virus has been isolated from various feral adult sockeye salmon populations (Guenther et al. 1959; Amend and Wood 1972; Grischkowsky and Amend 1976).

It would be difficult to prove that the disease is a problem in nature unless infected fish were found and associated with a documented decline in the population. At Chilko Lake, a tributary of the Fraser River, British Columbia (Fig. 1), dead fry are rarely found, even though extensive surveillance has been carried out during fry enumeration for about 25 yr. In the spring of 1973 an outbreak of IHN occurred at Chilko Lake. This report documents the first confirmed epizootic of IHN under natural conditions and indicates that the disease may have caused severe mortality among the 1972 brood sockeye salmon at Chilko Lake.

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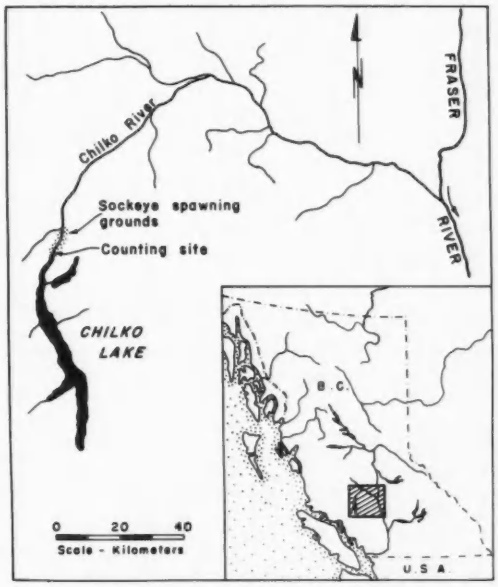

FIG. 1. Chilko Lake, Chilko River, British Columbia and spawning grounds of sockeye salmon (*Oncorhynchus nerka*).

Research

MORTALITY OF 1972 BROOD SOCKEYE SALMON POPULATION

During the fall of 1972, sockeye salmon deposited an estimated 1006.5 million eggs in the Chilko River system, 825.6 million in the Chilko River and 180.9 million near the shore of Chilko Lake. In the spring of 1973, 31.4 million fry migrated up the Chilko River and into the lake for a year's residence.

During the spring of 1973 a number of moribund and dead sockeye fry were observed in the Chilko River and Chilko Lake, as well as among captured fry being held in live boxes in the river. The majority of these fry exhibited clinical signs of IHN. Samples of the fry were later sent to the Western Fish Disease Laboratory for pathological examination which included a complete bacteriological and virological work-up. Small numbers of ubiquitous parasites and bacteria were found, but were considered of no consequence. However, in every sample of fry but one, IHN virus was isolated on fathead minnow (*Pimephales promelas*) cell cultures and its identity was confirmed by serological procedures developed by Amend (1970). All moribund fish examined histologically had lesions typical of IHN, confirming that the fish died of IHN disease.

In the spring of 1974 and 1975 an estimated 21.8 million smolts from the 1972 brood were counted on their seaward migration out of the lake. During the 1974 migration more smolts than usual were recovered dead or dying by the field crew, but examination of the fish showed no evidence of IHN virus.

MORTALITY OF 1973 SOCKEYE SALMON FRY

Fry began migrating up the Chilko River on May 5. The median date was May 29 and the run was essentially over by June 19 (Fig. 2). The mean water temperature during migration was 7.3 C. Both the timing of the run and the temperatures during migration were within the ranges observed for past Chilko fry migrations. About 38,000 fry captured on May 24 were transported live to the Sweltzer Creek (British Columbia) Research Laboratory. A few fry were dead or dying upon arrival and the mortality continued at a low rate through May 30. Mortalities increased sharply at the laboratory on May 31 and the fish were destroyed 6 days later, after a total of 8,169 (21.4%) of the fry had died.

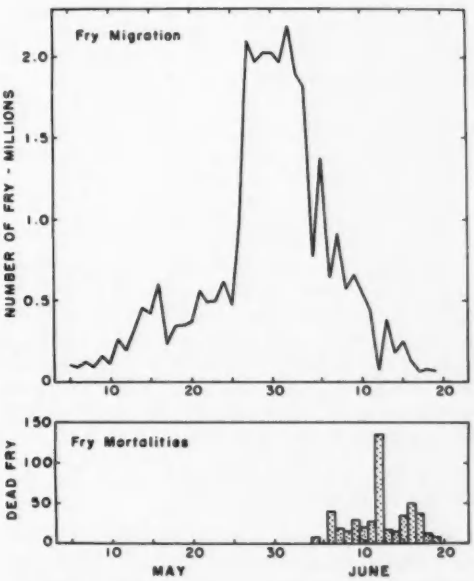

FIG. 2. Numbers of sockeye salmon fry migrating from the spawning grounds to Chilko Lake, and numbers of dead fry recovered, 1973.

Histopathological examination indicated IHN was the causative agent; however, IHN virus was not isolated from these fish. Additional fry were captured June 6 and transported to the Sweltzer Creek Laboratory. On June 14 a subsample of fry was sent to the Western Fish Disease Laboratory where IHN was confirmed. Subsequently, five samples of 50 fry were captured on June 17 and sent directly from Chilko Lake to the Western Fish Disease Laboratory. These included one sample of obviously stressed fish plus random samples from three areas of the Chilko River and one sample from Chilko Lake near the outlet. All five samples were confirmed positive for IHN. Field personnel also recovered 458 dead or moribund fry from Chilko River and Chilko Lake within a 2-wk period in June (Fig. 2). Many of these had one or more of the external signs of IHN including exophthalmia, hemorrhaging, and abdominal swelling. However, these numbers probably are not indicative of actual losses because many dead and moribund fry probably were eaten by predators or carried downstream.

An estimate of the mortality of migrating fry was determined from a sample of 20,300 fry captured June 15 and held only three days in a screened live box in the river. A total of 89 fry (0.44%) died or showed signs of IHN over the 3-day period. This rate of mortality is similar to the early rate (May 24–30) among the fish held at the Sweltzer Creek Laboratory. Even though there are no records of dead fry in the Chilko River itself before June, it appears probable that the virus was present at least from May 24 to the end of the migration.

Mortality of 1974 Sockeye Salmon Smolts

Through the entire 1974 smolt migration, more dead or dying smolts than usual, 5,446 or 0.025% of the total run, were recovered from the counting fence at Chilko Lake (Fig. 3). Field examinations of the fish revealed no signs of IHN, nor did virological examinations of fresh and preserved samples of moribund fish sent to the Western Fish Disease Laboratory.

Impact of the IHN Epizootic

Survival of sockeye salmon at Chilko Lake has been studied each year since 1949. A comparison of the dominant cycle years 1952–68 with 1972 indicates that survival of the 1972 brood was very poor. The survival of eggs-to-migrating fry was 3.8%, the lowest ever recorded from 1949 through 1973, and well below the dominant cycle

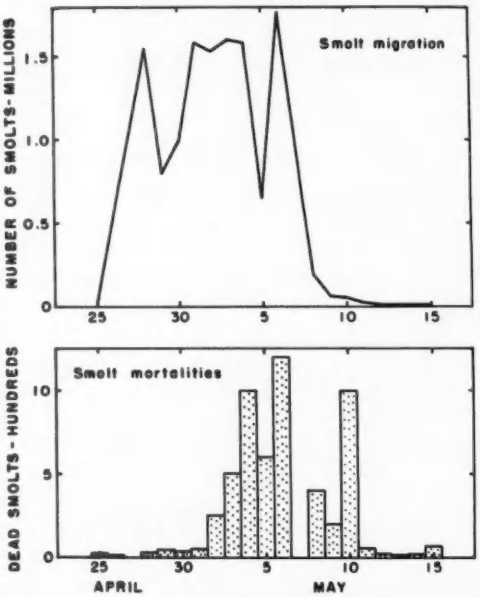

FIG. 3. Numbers of sockeye salmon smolts of the 1972 brood year migrating from Chilko Lake and number of dead smolts recovered, 1974.

average of 9.2%. The survival from fry-to-smolt for the 1972 brood was estimated at 57.1%, or somewhat higher than the mean of 51.9% for this cycle. However, the low egg-to-fry survival combined with the only slightly above average fry-to-smolt survival left an egg-to-smolt survival of only 2.16%, the lowest ever recorded at Chilko Lake and less than half the 4.99% average for the cycle.

The relation between the estimated numbers of eggs deposited in the river and the numbers of fry produced for the years 1952–71 at Chilko Lake is highly significant ($P = 0.01$). This relation indicates that fry production from the larger egg depositions was generally lower than that from the smaller egg depositions (Fig. 4). This correlation reflects compensatory mortality (limitation of spawning area) during spawning and incubation of sockeye salmon (Ward and Larkin 1964). The 1972 brood deviates furthest from the regression line representing the years 1952-71. According to the regression, 825.6 million eggs should produce 55.1 million fry. However, the estimated fry produced in the river was only 31.4 million, which is significantly lower than the predicted value at the 95% confidence level.

Although there were unusual mortalities of smolts at the counting fence, the number was

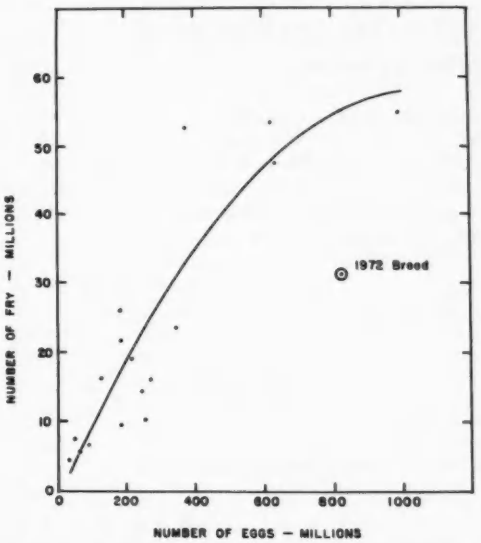

FIG. 4. Relation of fry produced from eggs deposited in Chilko River (not including Chilko Lake), 1952–71 as compared with numbers produced in 1972.

very small in proportion to the total run. No virus could be found in these fish, and the survival of fry-to-smolt was within the normal range. Therefore, IHN had no apparent effect on the fry during the lacustrine stage of the life cycle.

Discussion

Our data suggest that the IHN epizootic substantially reduced the Chilko sockeye salmon population and that the major impact occurred before or during the upriver migration of fry. The upriver migration itself may have removed many of the weakened fish before they reached the counting station and the lake. Although dead fry were recovered from the lake, IHN had no significant effect on mortality of the sockeye salmon during their lacustrine existence.

Acknowledgments

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Effects of Mercury and Copper on the Olfactory Response in Rainbow Trout, *Salmo gairdneri*

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HARA, T. J., Y. M. C. LAW, AND S. MACDONALD. 1976. Effects of mercury and copper on the olfactory response in rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 33: 1568–1573.

The effects of mercury and copper on the olfactory response of rainbow trout (*Salmo gairdneri*) were studied by perfusing $HgCl_2$ and $CuSO_4$ solutions through the olfactory organs while recording the olfactory bulbar electrical responses to the standard stimulant, L-serine.

The olfactory response was depressed during exposure to mercury and copper. The lowest concentrations of mercury and copper needed to cause appreciable effects within 2 h were estimated at 0.10 and 0.008 mg/liter, respectively. The depression increased with increase in the concentration and exposure time of the heavy metals. Recovery of the olfactory response was slower with higher concentrations and longer exposure.

The method is rapid, accurate, and sensitive, and can be applied to other toxic chemicals and fish species.

HARA, T. J., Y. M. C. LAW, AND S. MACDONALD. 1976. Effects of mercury and copper on the olfactory response in rainbow trout, *Salmo gairdneri*. J. Fish. Res. Board Can. 33: 1568–1573.

Nous avons étudié les effets du mercure et du cuivre sur la réponse olfactive de truites arc-en-ciel (*Salmo gairdneri*) par perfusion de solutions de $HgCl_2$ et de $CuSO_4$ dans les organes olfactifs et en enrégistrant en même temps les réponses électriques du bulbe olfactif au stimulant étalon, L'sérine.

La réponse olfactive est atténuée pendant l'exposition au mercure et au cuivre. Les concentrations minimums de mercure et de cuivre produisant des effets appréciables en dedans de 2 h sont estimées à 0.10 et 0.008 mg/litre respectivement. L'abaissement se fait plus prononcé à mesure qu'augmentent la teneur en métaux lourds et la durée d'exposition. Le rétablissement de la réponse olfactive est plus lent quand les teneurs sont plus élevées et la durée d'exposition plus longue.

La méthode est rapide, précise et sensible, et peut être appliquée à d'autres toxiques et à d'autres espèces de poisson.

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TOXICITY of mercuric and cupric salts to fish has been widely investigated since these metals were recognized as a serious problem in the aquatic environment. Laboratory bioassays have been designed to measure effects of toxic agents on survival, growth, and reproduction of fishes (Mount 1968; Mount and Stephan 1969; McKim and Benoit 1974; Eaton 1973). Although these tests are quite sensitive in detecting damage produced by sublethal concentrations of toxicants, a serious disadvantage with these end points is the large amount of time required to obtain useful information.

To supplement these long-term bioassay experiments, techniques that provide rapid information on organism responses to impaired water quality by the use of physiological measurements on fish have been developed (Kleerekoper et al. 1972, 1973; Eisler and Gardner 1973; MacLeod and Pessah 1973; Drummond et al. 1973; Gardner and LaRoche 1973). However, none of these studies has dealt with functional derangement of the chemosensory systems of fish caused by exposure to sublethal levels of mercury and copper.

Chemosensory receptors are immediate detectors of environmental chemical stimuli. Environmental changes are detected by transducer elements of the receptors and information is subsequently carried along nerve fibers to various integrating centers of the body. Olfaction plays an important role in the survival of fish. It

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mediates such diverse phenomena as feeding, recognition of prey and predator, sexual and social behavior, and orientation and migration (cf. Kleerekoper 1969; Hara 1970, 1971, 1975a). Since the olfactory membranes are not protected by external barriers, man-made alterations in the water quality could easily interfere with their functioning, the consequences being a breakdown in communication among fish and environment.

The present study was conducted to develop electrophysiological methodology to demonstrate acute effects at various sublethal concentrations of selected toxicants, mercury and copper, on the olfactory responses of rainbow trout (*Salmo gairdneri*) to a standard stimulant, L-serine, which is known to be an effective olfactory stimulant for this species (Hara 1975a, b, 1976).

Materials and Methods

Rainbow trout (*Salmo gairdneri*), ranging from 18.5 to 26.5 cm in body length, were used. They were obtained from a local hatchery, and held in large laboratory tanks supplied with a continuous flow of ultraviolet dechlorinated water (Armstrong and Scott 1974) for acclimation for more than 3 wk prior to use. The fish were immobilized with an intramuscular injection of Flaxedil (4 mg/kg body wt) after light anesthetization with M.S. 222 (ethyl *m*-aminobenzoate methanesulphonate) (1:8000 dilution), then secured in a plastic trough. The gills were perfused with water (1 liter/min, temperature 13 ± 0.5 C) throughout the experiments. (Total hardness of water used was 90 mg/liter as $CaCO_3$, average levels of Hg and Cu were 0.05 and 20 μg/liter, respectively, and the pH ranged from 7.5 to 7.8). The skin flaps separating anterior and posterior nares were removed, and the olfactory cavities were then perfused continuously with water (0.1 ml/naris per s), via paired glass capillaries (Fig. 1). Operative procedures on the fish and recording techniques of the electrical responses from the olfactory bulb have been described previously (Hara 1973).

L-serine at 10^{-5} M was used as a standard stimulus. The stimulant solution was delivered to the paired nares at the rate of 0.1 ml/naris per s for 10 s, at intervals of 2 min, using an automatic stimulatory apparatus (Fig. 1; Hara et al. 1973b). All measurements were taken after a stable maximum response to the standard stimulus was reached by repeated applications. Quantitative comparison of the responses under various conditions was made by measuring the total areas under the integrated curve (AC integration; Grass Model 7P3B; time constant, 0.5 s) or by measuring the maximum height of DC integration (Grass Model 7P10B) during the olfactory stimulation. Magnitude of the response was represented as a percentage of the control response before treatment.

An infusion pump was used to inject $HgCl_2$ and $CuSO_4$ solutions at the desired concentration into the main stream of water infusing the nares and gills of fish. Stock solutions of $HgCl_2$ and $CuSO_4$ were made up in D.W. (distilled water) and diluted as needed with same. The infusion rate of these solutions into the main stream of water was generally less than 10 ml/min. Thus, during exposure, water flowing into the nares and mouth and over the gills contained the toxicant. Water perfusing the nares was replaced by the stimulant solution for 10 s every 2 min. Essentially the same results were obtained when the heavy metal solutions were infused through the nares alone. In the present study, however, both nares and gills were infused throughout, because temperature and flow rate of solutions were better controlled under the condition illustrated in Fig. 1.

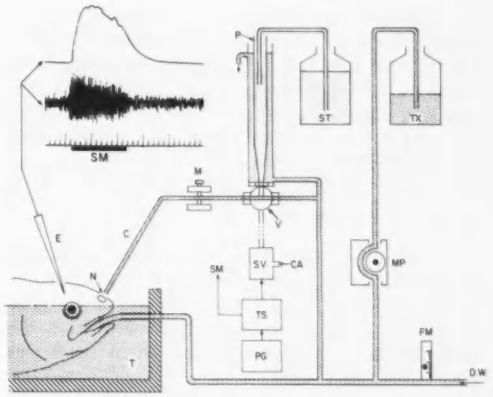

FIG. 1. Experimental setup for recording olfactory responses and for toxicant injecting system. The standard stimulant solution (ST) is led via plastic tubing into a glass pipette (P). By switching the three-way valve (V), the stimulant is poured into the nares (N) through a pair of glass capillaries (C) adjusted by a micromanipulator (M). CA, compressed air; D.W., dechlorinated water; E, recording electrodes; FM, flowmeter; MP, metering pump; PG, programmer; SM, signal marker; SV, solenoid valve; T, trough; TS, time switch; TX, toxic chemical solution.

In some cases the bulbar response was computer-analyzed in terms of its frequency components according to the method described in a previous report (Hara et al. 1973a). This describes amplitude of the response as a function of frequency rather than of time.

Results

Olfactory Bulbar Response to L-Serine

When the nares of fish were infused with a solution of L-serine, the background electrical activity (intrinsic waves) of the olfactory bulb was immediately interrupted by an oscillatory potential (induced response) that was terminated

by rinsing. The integrated bulbar-induced response normally increased exponentially with a logarithmic increase in stimulus intensity until the response reached maximum. For L-serine the response reached maximum at concentrations as low as 10^{-4} M. Further details have already been described elsewhere (Hara 1976).

Effects of Mercury

The bulbar response to L-serine normally started declining within the 1st 2 min after the injection of $HgCl_2$ into the water system. Figure 2 illustrates typical responses recorded from the olfactory bulb of the same fish when the nares were stimulated with 10^{-5} M L-serine before, immediately after exposure to 0.25 mg/liter $HgCl_2$ for 4 h, and after 1 h rinsing. The patterns of response and depression of response caused by $HgCl_2$ were qualitatively similar regardless of types of stimulants, such as other kinds of amino acids, food extracts, and hand rinse. No appreciable change in the background electrical activity was observed during exposure to toxicants under the present experimental conditions. With a more sensitive recording system, however, reduction in the amplitude of the background activity was also recognizable by brief application of mercury at comparable concentrations.

General patterns of the depressing effect of $HgCl_2$ on the bulbar response to the standard stimulant are shown in Fig. 3, where fish were treated with $HgCl_2$ for 2 h. Generally, an increase of $HgCl_2$ concentration increased the degree of depression of the response to the stimulus and increased the time required for recovery. For treatment with 0.25 and 0.30 mg/liter $HgCl_2$, the responses recovered to the original levels after 50- and 70-min rinsing. However, at much higher concentrations of $HgCl_2$ complete recovery did not occur even after rinsing for 2 h. At 0.40 and 0.50 mg/liter $HgCl_2$, for example, the responses recovered only to, respectively, 80 and 60% of the original levels after 2-h rinsing. For the same concentrations of $HgCl_2$, 0.25 mg/liter, the depression increased when the exposure time was prolonged, and the recovery accordingly became slower as shown in Fig. 4 and Table 1. The lowest concentration of $HgCl_2$ required to cause an appreciably depressing effect on the bulbar response within 2 h was estimated at 0.10 mg/liter (Fig. 5).

Computer analysis of the frequency components of the bulbar responses indicated little or no significant shift in the peak frequencies (mean, 7.8 Hz) after treatment with 0.25 mg/liter $HgCl_2$ for 4 h.

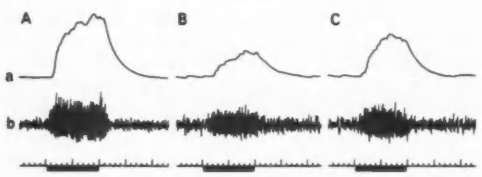

FIG. 2. Electrical responses recorded from the olfactory bulb of the same fish when the nares were stimulated with 10^{-5} M L-serine before (A) and after (B) exposure to 0.25 mg/liter $HgCl_2$ for 4 h, and 1 h after rinsing (C). The upper tracing (a) of each pair is the integrated responses of the lower (b). Duration of stimulation is indicated by heavy lines below each record. Time scale, each division = 1 s.

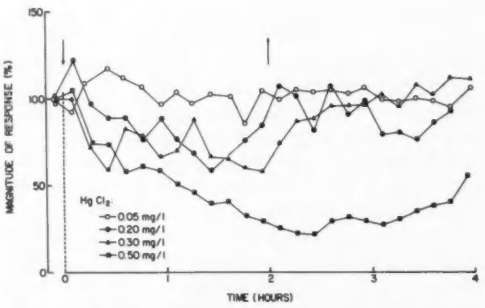

FIG. 3. Time change of the olfactory responses to the standard stimulant 10^{-5} M L-serine when fish are exposed to 0.05, 0.20, 0.30, and 0.50 mg/liter $HgCl_2$ for 2 h. ↓ indicates onset of treatment and ↑ commencement of rinsing. The magnitude of the responses in this and the following figure is represented as a percentage of that of the control response before treatment.

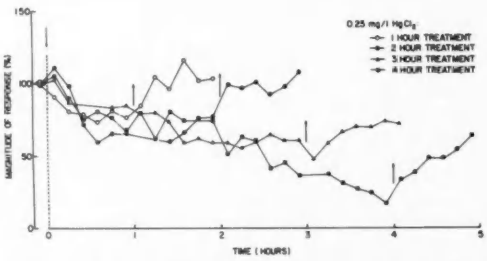

FIG. 4. Effects of duration of treatment. Fish were treated with 0.25 mg/liter $HgCl_2$ for 1, 2, 3, and 4 h, respectively. Note that the depression continues during exposure. Arrows delimit periods of treatment.

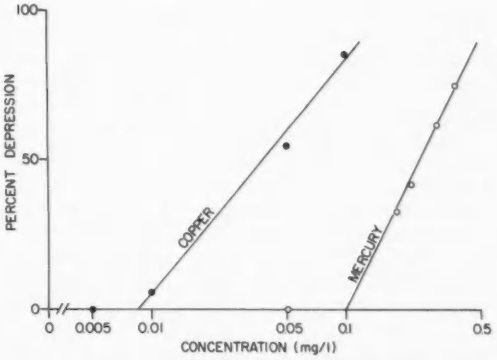

FIG. 5. Relationship between percent depression and concentrations of $HgCl_2$ and $CuSO_4$. Fish were treated for 4 h.

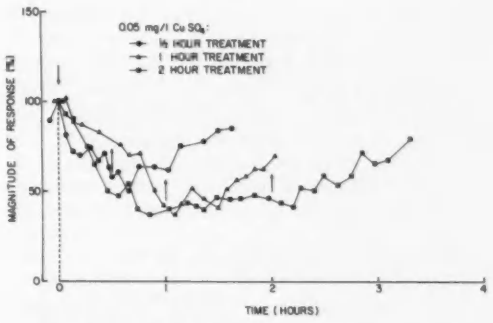

FIG. 6. Olfactory bulbar responses to standard stimulant L-serine when the nares were exposed to 0.05 mg/liter $CuSO_4$ for ½, 1, and 2 h.

TABLE 1. Relationships between exposure time (0.25 mg/liter $HgCl_2$) and the magnitude of response to 10^{-5}M L-serine, and recovery after rinsing. The response is represented as a percentage of that of the control.

Duration of exposure (*h*)	Response at the end of exposure (%)	Recovery after rinsing
1	77.5	To 100% in 20 min
2	67.0	" 100% " 50 "
3	47.0	" 60% " 60 "
4	28.5	" 55% " 60 "

EFFECTS OF COPPER

Copper sulphate had more depressing effects on olfactory response than $HgCl_2$ at the same concentration. With 0.05 mg/liter Cu, for example, the response was depressed to approximately 55% of the original level after a 2-h treatment. Complete recovery was not achieved even after rinsing for 2 h with dechlorinated water (Fig. 6). The threshold concentration of copper needed to cause minimal depression of the bulbar response was determined to be 0.008 mg/liter added to the laboratory water, which is 12.5 times lower than that for $HgCl_2$ (Fig. 5).

Discussion

The results clearly indicate that the olfactory responses to the standard stimulant in rainbow trout can be depressed by mercury and copper at sublethal concentrations. The lowest concentrations of mercury and copper to cause appreciable effects within 2 h were estimated at 0.10 and 0.008 mg/liter, respectively. These are approximately 3 and 5 times lower than their respective lethal levels for rainbow trout (MacLeod and Pessah 1973; Lloyd and Herbert 1962). It is unknown what percentage of the total $HgCl_2$ and $CuSO_4$ added was Hg^{++} and Cu^{++}. The fraction of each that is ionized will depend on pH, water hardness, time after mixing, and total ionic content, etc. Copper is also highly complexed by carbonate and hydroxide ions in natural waters and this complexing determines the concentration of copper species in solution (Pagenkopf et al. 1974). Since it is probably the metal ions that are active, the threshold is probably lower than those estimated above. Furthermore, since the degree of depression increased with increase in exposure time, the threshold concentrations estimated above could be reduced.

There are several ways in which these heavy metals might interact with olfactory receptors, thus resulting in reduction of sensitivity or elevation of the threshold for detection of odorous chemicals in water. Most pertinent is probably cell impairment due to membrane dysfunction caused by binding or coupling between the heavy metals and the receptors. The effects of mercury and copper as blocking agents have been demonstrated in many chemosensitive systems (Yur'eva 1957; Hidaka and Yokota 1967; Hidaka 1970; Sutterlin and Sutterlin 1970, 1971; Yamamoto and Kawamura 1971a, b; Hara 1972). The rapid depression of the olfactory bulbar responses by exposing the olfactory organs to $HgCl_2$ or $CuSO_4$, and the rapid recovery by rinsing suggest that the reaction may take place on the receptor membrane and perhaps on the receptor site. Mercuric and cupric ions are known to tie up, respectively, sulfhydryl and amino groups of proteins. The blocking effect observed here may be due to interference with these reactive groups of the receptor membranes. In the olfac-

tory epithelium of rainbow trout, a receptor site that involves two charged subsites capable of binding with ionized amino and carboxyl groups of stimulant amino acids has been proposed (Hara 1975a, b). Furthermore, recent electrophysiological studies suggest that sulfhydryl groups are involved in olfaction in fish. The electrical responses of the olfactory bulb of rainbow trout to amino acids are inhibited by a sulfhydryl agent, N-ethylmaleimide (NEM) at 10^{-4} M (T. J. Hara unpublished data). Specificity of this inhibitory effect was also confirmed in the experiments in which 2-mercaptoethanol, when simultaneously applied, protected the inhibition by NEM. Such inhibition or reduction by NEM of nervous responses to stimulation of chemoreceptors are reported in other animal species (Hidaka 1970; Koyama and Kurihara 1971; Getchell and Gesteland 1972).

Kleerekoper et al. (1972, 1973) reported that goldfish (*Carassius auratus*) responded to sublethal concentrations of copper (11–17 μg/liter) by modifying their locomotor characterisitcs in an open field. Depending upon the steepness of the concentration gradient and the availability of other sensory cues, goldfish could either avoid or be attracted to these levels of copper. Atlantic salmon (*Salmo salar*) smolts avoided copper sulphate at the threshold concentration of 2.3 μg/liter (Sprague 1964). The degree of toxicity and the avoidance level of many pollutants do not seem to be related, and many pollutants are not avoided at concentrations exceeding the lethal level (see Sprague and Drury 1969). Drummond et al. (1973) observed the change in cough frequency, locomotor activity, and feeding behavior when yearling brook trout (*Salvelinus fontinalis*) were exposed to copper at concentrations of 6–15 μg/liter for 2–24 h. Although these tests are quite sensitive in detecting behavioral changes caused by copper, the indirect nature of the studies makes it difficult to pinpoint the loci of the effects and the underlying physiological mechanisms.

Studies on water selection using adult migrating Atlantic salmon have shown that low levels of copper (44 μg/liter) alter the effectiveness of homestream water as an attractant (Sutterlin and Gray 1973). It is uncertain whether this is due to the pronounced avoidance of this metal by salmon or to reduced responsiveness to homestream water by the damaged receptors. In any case these studies raise the possibility that such metals may somehow interfere with the perception of the normal homestream odor that guides salmon to the spawning tributary. The use of olfactory cues by salmon in homing to and within rivers appears well established (for reviews see Jones 1968; Hara 1970; Hasler 1971).

Exposure to 0.5–5.0 mg/liter copper, admittedly high, for 6–24 h permanently damaged the olfactory mucosa of some estuarine fishes (Gardner and LaRoche 1973). Persistent binding of heavy metals to receptor sites at sublethal concentrations may also result in irreversible damage to the receptor cells.

The electrophysiological method described here is a sensitive, fast, and highly specific bioassay. This method can also be applied to other toxicants and to other fish species. However, it could be even more useful in combination with behavioral, histological, and biochemical approaches by showing exactly how the decrease in olfactory sensitivity affects behavior and whether or not damage at the cellular and molecular levels occurs.

Acknowledgments

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Distribution, Age and Growth, and Sexual Maturity of Witch Flounder (*Glyptocephalus cynoglossus*) in Newfoundland Waters

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BOWERING, W. R. 1976. Distribution, age and growth, and sexual maturity of witch flounder (*Glyptocephalus cynoglossus*) in Newfoundland waters. J. Fish. Res. Board Can. 33: 1574–1584.

Witch flounder (*Glyptocephalus cynoglossus*) were caught from the Hawke Channel to the southern edge of the Grand Bank and west to the Scotian Shelf and the Gulf of St. Lawrence. Although the largest catches were taken at 2–6 C and 185–370 m, witch flounder were found at temperatures ranging from −1 to 10 C and depths of 20–870 m. Witch flounder of the Northeast Newfoundland Shelf were largest and those of the Gulf of St. Lawrence smallest at comparable ages, with growth rates for the east coast of Newfoundland being faster than most other areas. Age and length at 50% sexual maturity ranged from 4.20 to 5.59 yr and 25 to 30 cm for males, and from 8.42 to 10.21 yr and 40 to 50 cm for females.

BOWERING, W. R. 1976. Distribution, age and growth, and sexual maturity of witch flounder (*Glyptocephalus cynoglossus*) in Newfoundland waters. J. Fish. Res. Board Can. 33: 1574–1584.

On a capturé des plies grises (*Glyptocephalus cynoglossus*) à partir du chenal Hawke jusqu'à l'accore méridionale du Grand banc et vers l'ouest jusqu'au plateau Néo-écossais et le golfe Saint-Laurent. Bien que les plus grosses prises aient été faites à des températures de 2–6 C et à des profondeurs de 185–370 m, on a trouvé des plies grises à des températures allant de −1 à 10 C et à des profondeurs de 20–870 m. A des âges comparables, les plies grises du nord-est du plateau terre-neuvien sont les plus grandes et celles du golfe Saint-Laurent les plus petites, le rythme de croissance sur la côte orientale de Terre-Neuve étant généralement plus rapide que celui des autres régions. L'âge et la longueur auxquels 50% des individus atteignent la maturité sexuelle sont de 4.20 à 5.59 a. et de 25 à 30 cm pour les mâles, et de 8.42 à 10.21 a. et de 40 à 50 cm pour les femelles.

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THE purpose of this paper is to present information on distribution of witch flounder (*Glyptocephalus cynoglossus*) principally in waters adjacent to Newfoundland and to provide information on the age composition and growth patterns for different localities in which it occurs. Special emphasis will be placed on difference in growth between areas and associated differences in size and age at the onset of sexual maturity.

Information on the biology of this species in the northwest Atlantic is limited. Powles and Kohler (1970) published information on depth distribution of various stages of witch flounder but confined their study to areas off Nova Scotia and in the Gulf of St. Lawrence. Evseenko and Nevinsky (1973) presented a detailed study of breeding and development of witch flounder in the whole northwest Atlantic area and Powles and Kennedy (1967) published data on age validation of witch flounder from otoliths. Markle (1975) introduced new information on young witch flounder on the slope off Virginia.

Although a large proportion of the catch of witch flounder is taken as a by-catch of other fisheries, it forms an important component of Newfoundland's groundfish resource (Templeman 1966). The fishery for witch flounder began in the late 1940s with the establishment of the local otter-trawling fleet in Newfoundland. Exclusive fishing occurred in Fortune Bay using Danish seines in the early 1950s, and in St. George's Bay from 1956 when low catches forced the seiners to move from Fortune Bay. The witch flounder fishery was essentially a by-product of the haddock fishery in the late 1950s and early 1960s on the southwest slope of the Grand Bank (Templeman 1966). Since the decline in the

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haddock (*Melanogrammus aeglefinus*) fishery, witch flounder became a by-catch of Atlantic cod (*Gadus morhua*) and American plaice (*Hippoglossoides platessoides*) on the Grand Bank, the cod fishery on the Northeast Newfoundland Shelf and southern Labrador, and the fishery for cod and redfish on St. Pierre Bank. In the Gulf of St. Lawrence, witch flounder is mainly a by-catch of the fishery for redfish with some taken by Danish seiners in the area off Cape Breton Island. In recent years, witch flounder has become a major species utilized by inshore fishermen of Notre Dame Bay and in Trinity Bay as a result of declines in catches of cod and Greenland halibut (*Reinhardtius hippoglossoides*) (Bowering and Pitt 1974).

Materials and Methods

Most data were collected during all seasons on survey cruises of the 168-ft side trawler *A.T. Cameron*, operated by the St. John's Biological Station during 1958–74, using a 41-5 Yankee otter trawl equipped with nylon liner in the codend having a 127–281-mm mesh size. Only catch records of sets in which no damage to gear occurred were used in presenting information on distribution. Growth curves for Hermitage Bay and Fortune Bay, and distribution in Fortune Bay, were computed from material collected during gear experiments of the 60-ft side trawler *Marinus*, using a 35A otter trawl with a similar lining in the codend. Areas referred to in text are presented in Fig. 1.

Distribution

The geographic distribution and relative abundance of witch flounder are presented by indicating in ½° lat. and 1° long. rectangles, average weights of fish caught per 30-min tow per rectangle. Numbers of fish could not be used as an index of abundance because in most cases only weights were recorded. The numbers of fishing sets used to plot the distribution chart are presented in Fig. 2. Data for distribution by depth and temperature were combined for all survey areas.

Aging Techniques

Age was determined from the left sacculus otolith which appeared to be most suitable because the annuli were spaced more evenly and were more distinct. Otoliths were ground on the convex surface thus exposing the center and were placed in a black watchglass containing ethanol. Validity of age determination in witch flounder has been documented by Powles and Kennedy (1967).

Growth Curves

Growth curves of witch flounder were presented for each of eight different areas to show the gradual change in growth patterns throughout the whole region. They were illustrated by the inverse exponential equation in the von Bertalanffy form obtained by a least squares fit to the mean length at age for males and females separately (von Bertalanffy 1938). The form of the von Bertalanffy equation used is:

$$l_t = L_\infty(1 - e^{-K(t-t_0)})$$

where: l_t = length of fish (centimeters at age t years)
L_∞ = theoretical maximum length
K = constant expressing relative rate of growth
t_0 = theoretical age at which $l_t = 0$

To compare growth rates and how they change with age, a semilogarithmic plot of $\frac{dl}{dt}$ against t (Sandeman 1969) of the equation

$$\frac{dl}{dt} = KL_\infty e^{-K(t-t_0)}$$

was used to give

$$\log_e \frac{dl}{dt} = \log_e K + \log_e L_\infty + K(t - t_0)$$

The latter equation, when plotted on semilogarithmic paper, gives a straight line fit that illustrates growth rate on an instantaneous basis.

Age and Size at Sexual Maturity

Because of data limitations, comparisons of age and size at sexual maturity were presented for four major areas instead of the eight areas used on growth comparisons: Gulf of St. Lawrence (International Commission for the Northwest Atlantic Fisheries [ICNAF] Divisions 4RS), St. Pierre Bank (ICNAF Division 3Ps), Southwest Grand Bank (ICNAF Divisions 3NO), and Southern Labrador and Northeast Newfoundland Shelf (ICNAF Divisions 2J-3KL). Ages at which 50% of the fish are sexually mature (M_{50}) for each area by sex was calculated by probit analysis (Bliss 1952) as applied by Fleming (1960) for cod and Pitt (1966) for American plaice. Lengths at M_{50} were read directly from growth curves using calculated ages at M_{50}.

Results

Geographic Distribution and Relative Abundance

In survey catches, witch flounder were caught from the Hamilton Inlet Bank area (ICNAF Division 2J) southward to the Scotian Shelf (ICNAF Divisions 4VWX) and into the Gulf of St. Lawrence (ICNAF Divisions 4RST) (Fig. 3).

To the north, greatest quantities of witch flounder were caught in Hawke Channel. Approximately 2300 kg and 1400 kg/30-min tow were caught in two sets at depths of 164 and

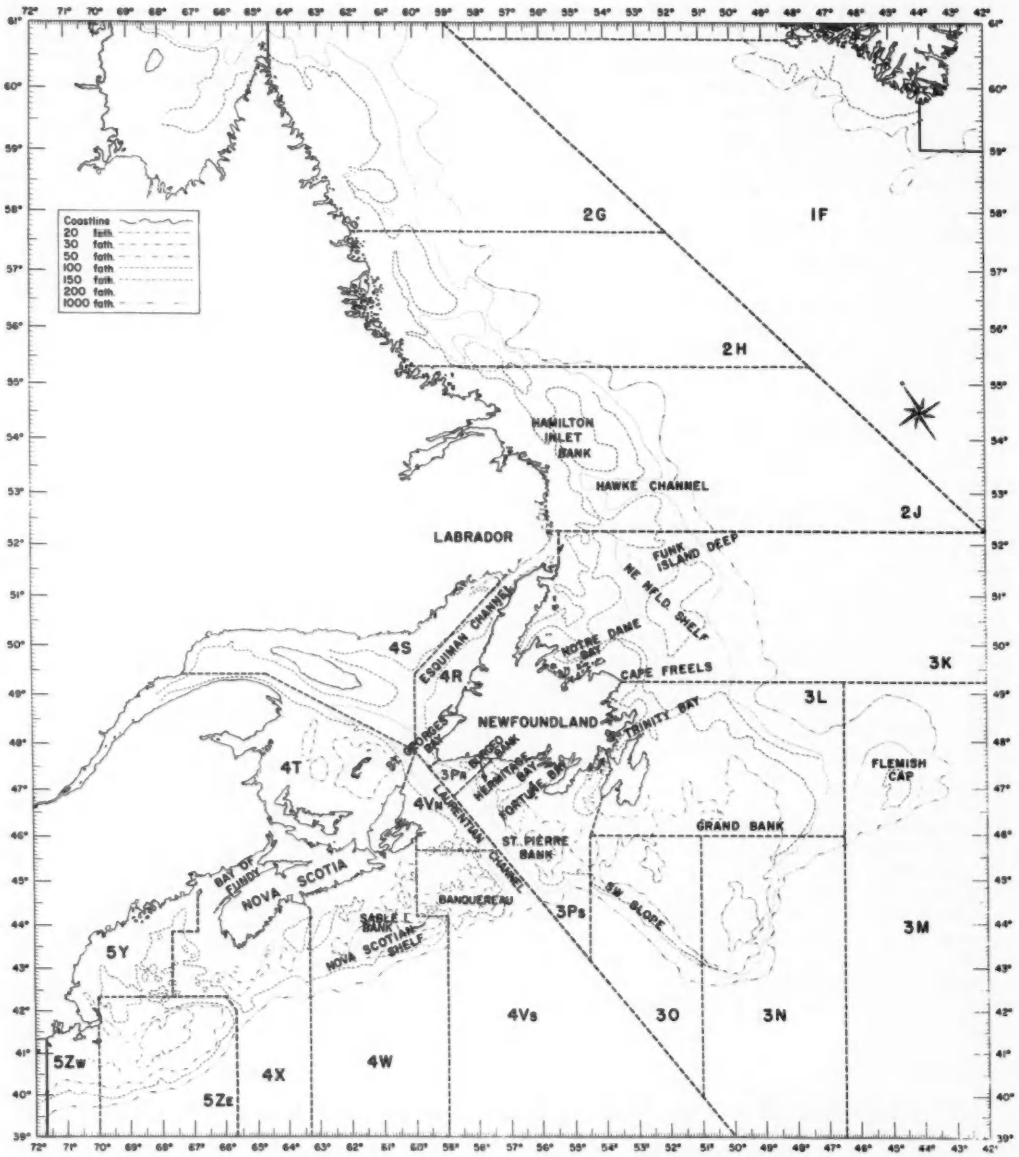

FIG. 1. Place names, fishing areas, and ICNAF areas referred to in the text.

191 m, respectively, in April 1963. In April 1964 in the same area, the *A.T. Cameron* in one 30-min tow caught 3300 kg of witch flounder. Large catches (averaging 15–46 kg/30-min tow) in the eastern Newfoundland area occurred on the Northeast Newfoundland Shelf (ICNAF Division 3K) with largest catches averaging 5–99 kg/30-min tow) occurring east of Cape Freels. Similar quantities were taken on the deep northern part of the Grand Bank with catches less than 1 kg recorded on shallower parts of the Bank. Consistently large catches (averaging 11–47 kg/30-

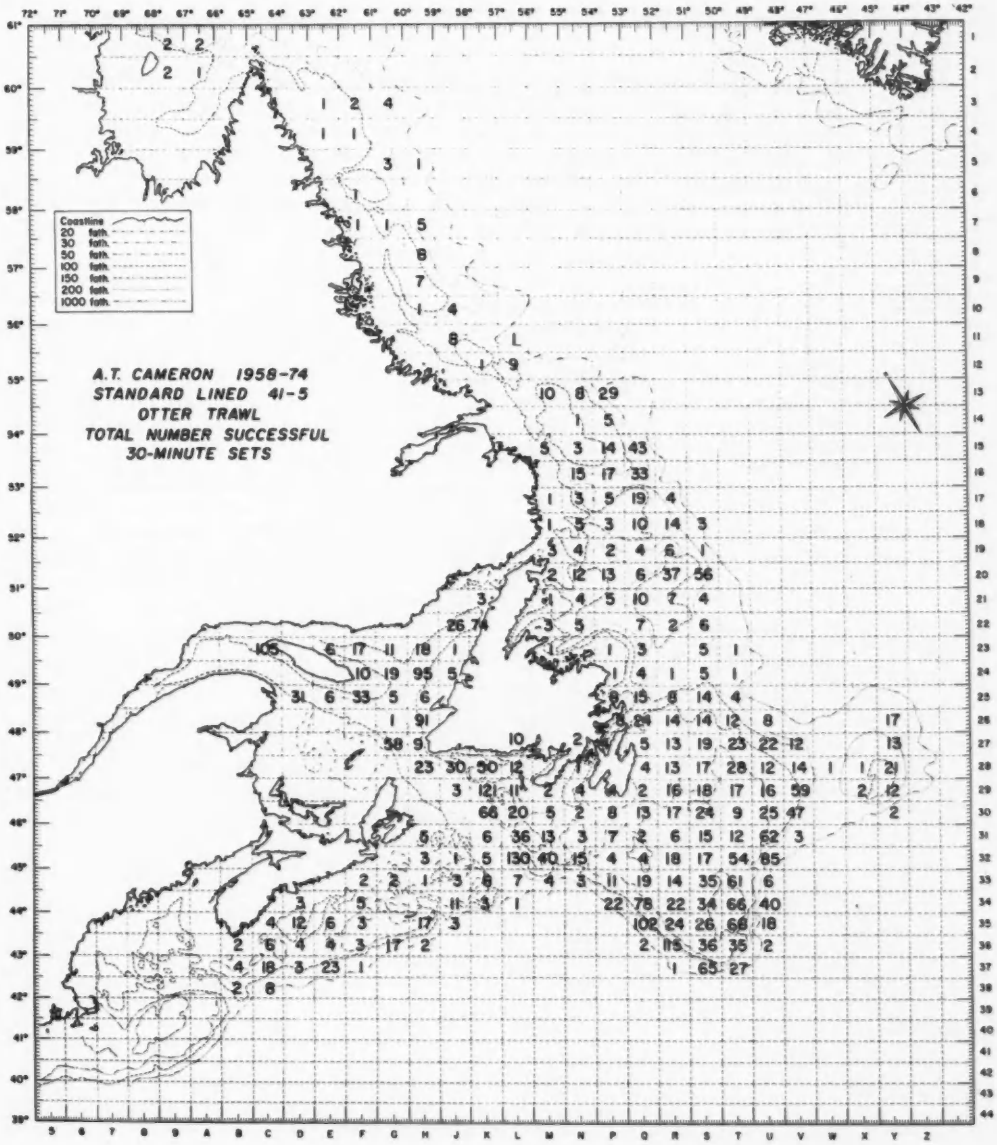

FIG. 2. Number of successful otter-trawling sets of the research vessel *A. T. Cameron*, 1958–74.

min tow) were found along the deep muddy southwest slope of the Grand Bank. Small concentrations of witch flounder occurred along the southern slope of St. Pierre Bank and Burgeo Bank with catches averaging 10–45 kg/30-min tow. A research survey by the *Marinus* in 1974 indicated very low quantities of witch flounder in Fortune Bay with catches averaging 6–8 kg/30-min tow. In most areas on the Scotian Shelf, localized areas of high abundance occurred along the edge of the Laurentian Channel, between Sable Island and Banquereau Banks, in the deep holes of Banquereau and at the mouth of the Bay of Fundy. Catches along the Shelf averaged 13–35

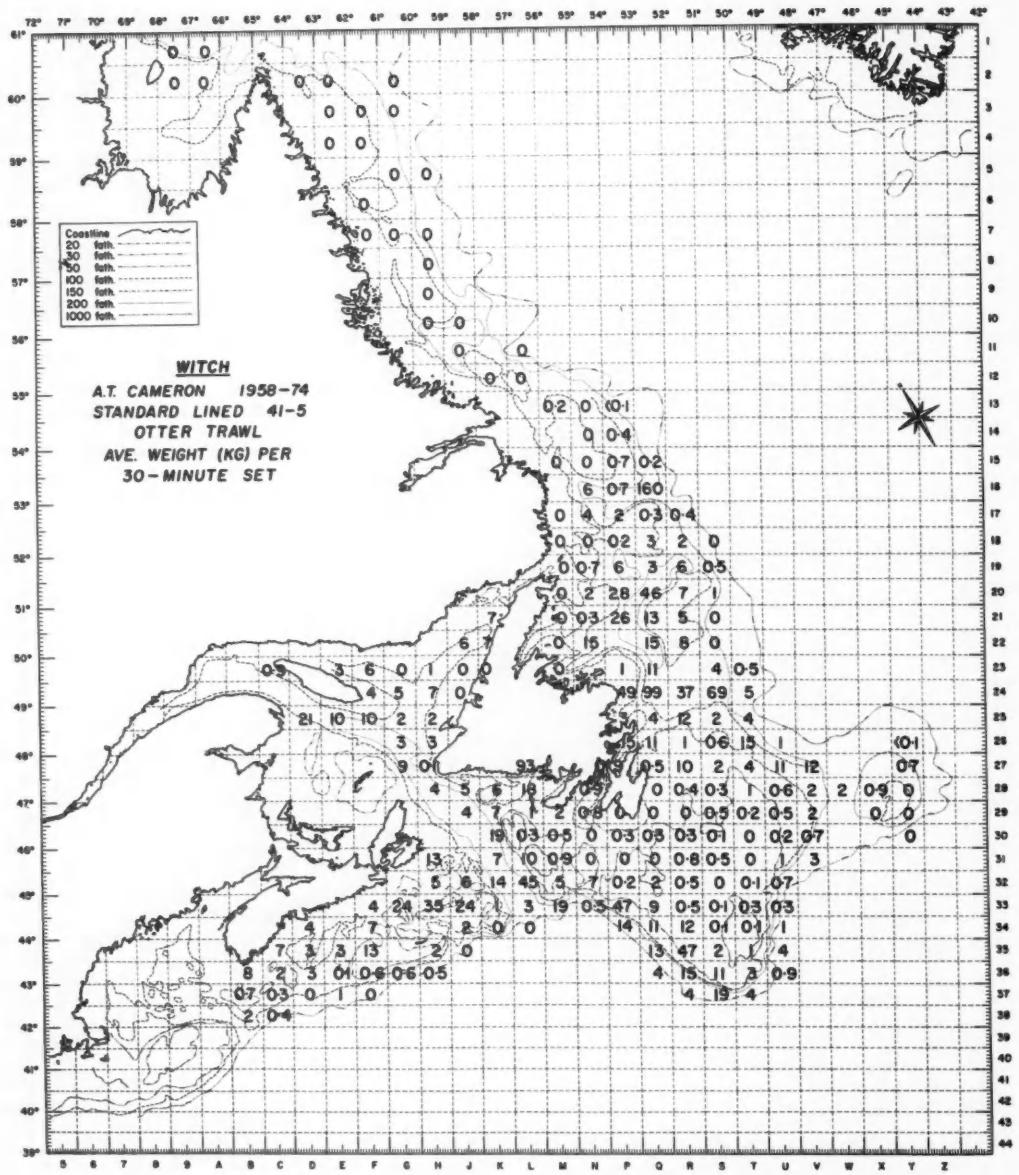

FIG. 3. Average catch of witch flounder (kilograms whole weight) by ½° lat. 1° long. rectangles per 30-min otter-trawling set of the *A. T. Cameron*, 1958–74.

kg/30-min tow. Witch flounder were found throughout the Gulf of St. Lawrence, including the Esquiman Channel with largest catches (10–21 kg/30-min tow) south of Anticosti Island (ICNAF Divisions 4S and 4T).

DISTRIBUTION BY DEPTH AND TEMPERATURE

Witch flounder were caught from 20 to 870 m with greatest abundance at 185–366 m and occurred at temperatures ranging from −1.0 to

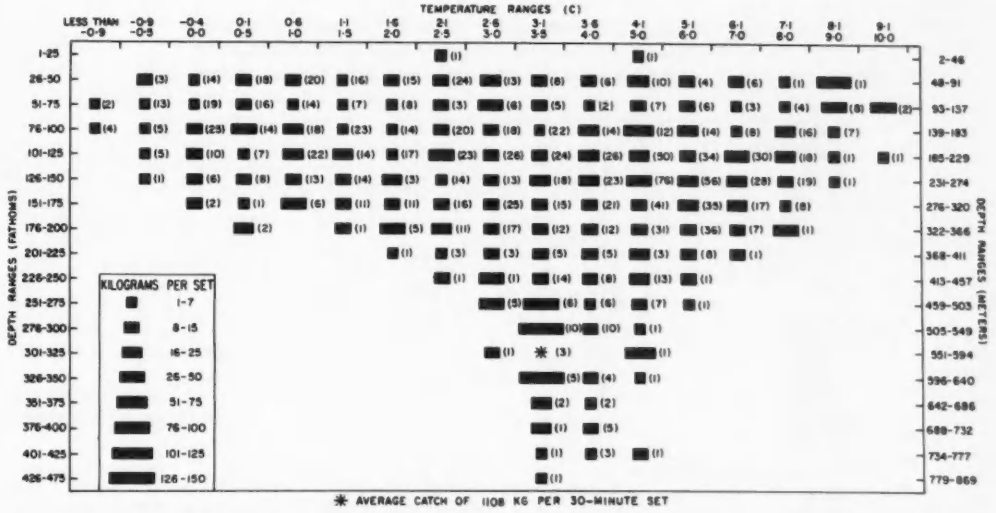
TEMPERATURE RANGES (C)
DEPTH RANGES (FATHOMS)
DEPTH RANGES (METERS)
KILOGRAMS PER SET
AVERAGE CATCH OF 1108 KG PER 30-MINUTE SET

FIG. 4. Average catch of witch flounder (kilograms whole weight) per 30-min otter-trawling set of the *A. T. Cameron* at various depths and bottom temperatures, 1958–74. Numbers in parentheses refer to the number of sets completed.

10.0 C (Fig. 4). The largest catches (780 kg, 1200 kg, and 3320 kg) per 30-min tow were taken at bottom temperatures of 3.1–3.5 C in the southern Labrador area. The temperature range at which greatest catches were taken was from 2 to 6 C for the study area as shown in the following table.

Area	Temp range for largest catches (C)
Gulf of St. Lawrence (4RS)	4.1–5.0
St. Pierre Bank (3Ps)	4.1–6.0
Southern Grand Bank (3NO)	3.1–4.0
Northern Grand Bank (3L)	3.1–5.0
NE Nfld. Shelf (3K)	2.1–5.0
Hamilton Inlet Bank and Hawke Channel (2J)	3.1–3.5

AGE AND GROWTH

Total growth of females was always greater than that of males and among older fish females were always larger than males (Fig. 5). The major differences between the sexes is the growth parameter L_∞. The L_∞ in conjunction with confidence limits for males and females of each area showed no overlap of the sexes except for St. Pierre Bank males where there was a large standard error. This indicated that the differences in L_∞ are likely to be real (Table 1); also, parameters K and t_0 of the growth equation showed few differences.

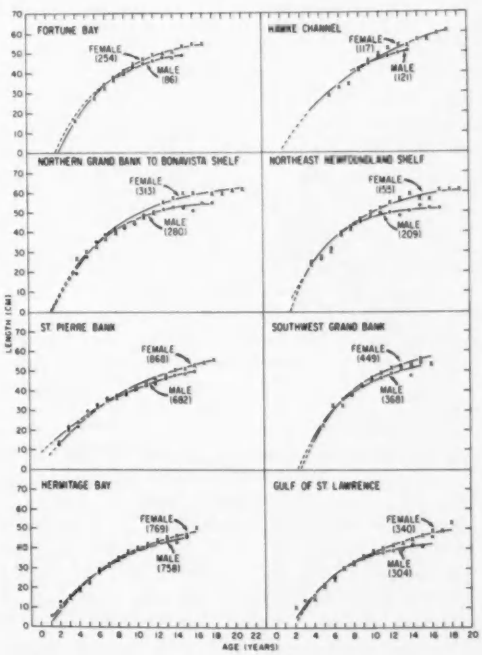

FIG. 5. Growth curves of male and female witch flounder from eight Newfoundland areas. Broken lines are extrapolated values.

TABLE 1. Parameters for von Bertalanffy growth curves with standard error for male and female witch flounder (*Glyptocephalus cynoglossus*) for eight Newfoundland areas.

	K	L_∞	t_0
Hermitage Bay			
Males	0.150±0.011	52.051±1.502	0.068±0.159
Females	0.126±0.006	56.891±1.161	0.435±0.124
Gulf of St. Lawrence			
Males	0.232±0.025	44.201±1.127	0.864±0.324
Females	0.136±0.023	54.920±3.168	0.296±0.510
St. Pierre Bank			
Males	0.099±0.020	60.492±4.690	−1.346±0.696
Females	0.111±0.013	63.80 ±2.672	−0.017±0.376
Southwest Grand Bank			
Males	0.212±0.067	55.891±3.801	1.441±1.090
Females	0.192±0.030	61.931±2.450	1.690±0.520
Northern Grand Bank			
Males	0.205±0.048	56.651±2.563	1.428±0.980
Females	0.156±0.027	65.530±2.793	1.363±0.753
NE Newfoundland Shelf			
Males	0.269±0.029	52.582±1.059	0.784±0.314
Females	0.164±0.022	64.688±2.342	0.198±0.420
Hawke Channel			
Males	0.130±0.011	58.010±1.526	−2.203±0.354
Females	0.101±0.010	74.021±2.027	−0.292±0.520
Fortune Bay			
Males	0.210±0.013	52.301±2.154	1.901±0.311
Females	0.182±0.020	58.512±1.256	2.281±0.105

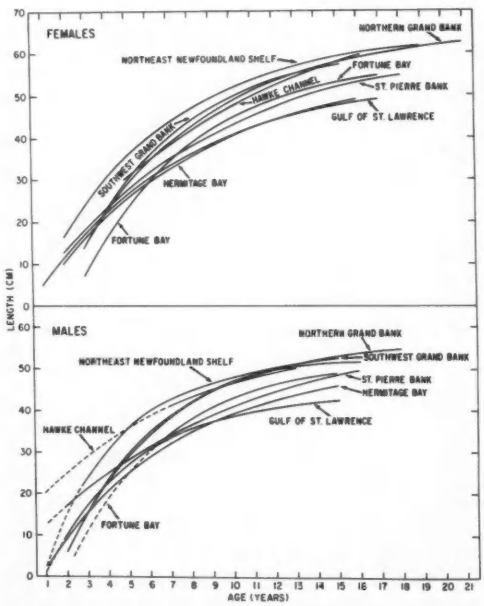

FIG. 6. Comparisons of growth curves of male and female witch flounder from eight Newfoundland areas. Broken lines are extrapolated values.

The fastest growth occurred in the Northeast Newfoundland Shelf area (Fig. 6; Table 1) for both males and females. However, growth patterns were generally similar for an area extending from Hawke Channel to the southwest slope of the Grand Bank. Witch flounder from St. Pierre Bank, Fortune Bay, Hermitage Bay, and the Gulf of St. Lawrence had growth curves that were also similar to each other but they were generally smaller at age than in the former areas. Except for the males of St. Pierre Bank, the L_∞ for males and females was larger for Hawke Channel to southern Grand Bank areas than that recorded for St. Pierre Bank west to the Gulf of St. Lawrence areas (Table 1). The fastest rate of growth for males was in Fortune Bay (Fig. 7). The slowest rate of growth for males was in Hawke Channel to approximately age 8, but beyond this, males from Northeast Newfoundland Shelf had slowest growth.

The fastest rate of growth in the females occurred on the southwest slope of the Grand Bank up to approximately age 8 but beyond this, females from Hawke Channel showed the fastest growth rate (Fig. 7). Early growth is slowest in the St. Pierre Bank area until age 3 but beyond this, the Gulf of St. Lawrence showed the slowest growth rate until about age 13. Beyond age 13,

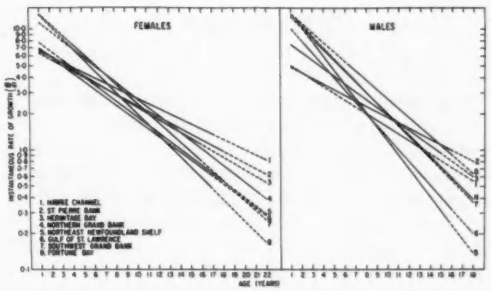

FIG. 7. Growth rate plotted against age for male and female witch flounder for eight Newfoundland areas. – – – –, extrapolated values.

the slowest growth for female witch flounder is in Fortune Bay.

SEXUAL MATURITY

Males — The age at 50% maturity ranged from 4.20 yr in Hawke Channel–Northeast Newfoundland Shelf to 6.20 yr in the Gulf of St. Lawrence (Fig. 8). The ages at 50% maturity of males from St. Pierre Bank (5.05) and Northeast Newfoundland Shelf (4.20) were not statistically different. The ages at 50% maturity of the Gulf of St. Lawrence (6.20) and the southwest Grand Bank (5.59) did not differ. However, the age at 50% maturity for the Gulf of St. Lawrence was statistically different from all other areas ($P \leq 0.02$). The age at the onset of sexual maturity ranged from 4 yr in Hawke Channel and Northeast Newfoundland Shelf to 6 yr in the Gulf of St. Lawrence and southwest slope of the Grand Bank areas (Fig. 9). Age at which all

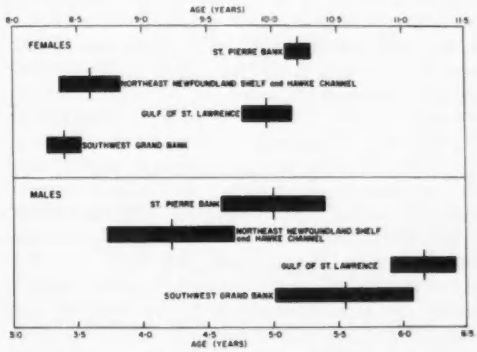

FIG. 8. Ages at which 50% of male and female witch flounder mature in four major areas around Newfoundland. The vertical bar is the mean; the rectangle is twice the standard error of the mean.

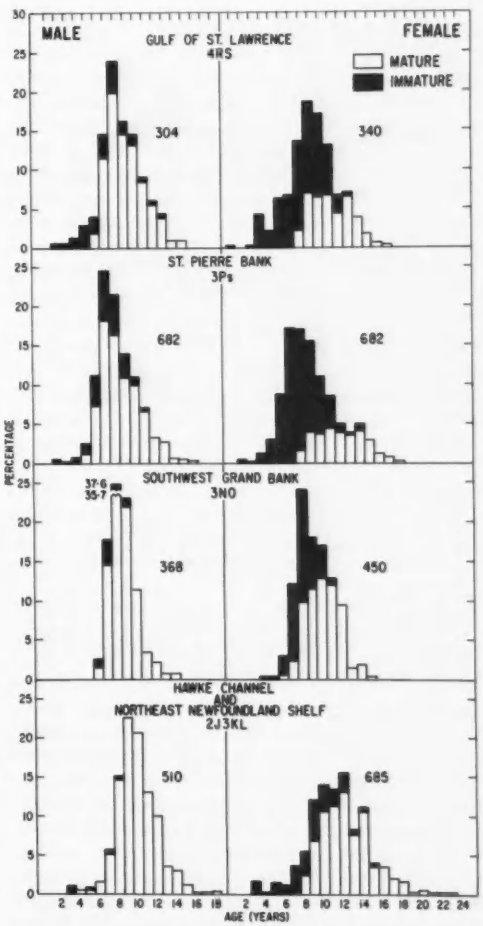

FIG. 9. Distribution of mature and immature male and female witch flounder according to age for four major Newfoundland areas. Numbers of fish sampled are indicated on the figure.

were mature ranged from 9 yr for Hawke Channel–Northeast Newfoundland Shelf area to 13 yr in the Gulf of St. Lawrence area.

Length of males at M_{50} ranged from 25 cm in the Gulf of St. Lawrence to 30 cm in the Northeast Newfoundland Shelf and Hawke Channel (Fig. 10). The lengths at M_{50} for the southwest Grand Bank and St. Pierre Bank were 29 and 28 cm, respectively. Length at first maturity ranged from 22 cm on St. Pierre Bank to 30 cm in Hawke Channel and Northeast Newfoundland Shelf (Fig. 10). All male witch flounder were mature at 43 cm in the Gulf of St. Lawrence and 47 cm in the southwest slope of the Grand Bank.

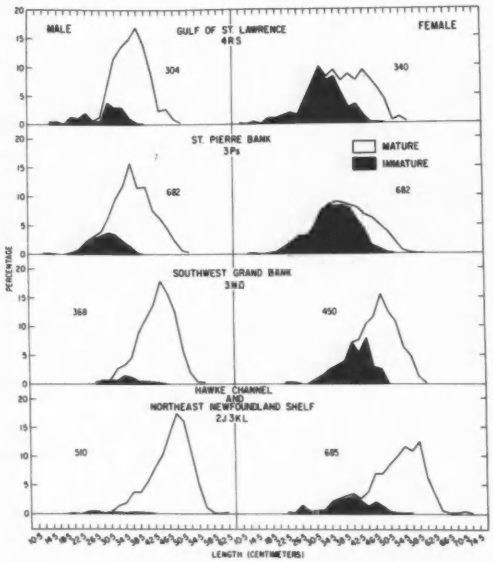

FIG. 10. Distribution of mature and immature male and female witch flounder according to length for four major Newfoundland areas. Numbers of fish sampled are indicated on the figure.

Females — Age at 50% maturity ranged from 8.42 yr on the southwest slope of the Grand Bank to 10.21 yr on St. Pierre Bank (Fig. 8). The ages at 50% maturity of females from the Hawke Channel–Northeast Newfoundland Shelf (8.62) and the southwest slope of the Grand Bank (8.42) were not statistically different ($P > 0.05$). Although the values for females from St. Pierre Bank (10.21) and the Gulf of St. Lawrence (9.95) were not statistically different ($P > 0.05$), both were statistically different ($P \leqslant 0.05$) from those females from Hawke Channel–Northeast Newfoundland Shelf and St. Pierre Bank. The age at the onset of sexual maturity (Fig. 9) ranged from 6 yr on the southwest Grand Bank to 8 yr in the Gulf of St. Lawrence. Ages at which all females reached sexual maturity ranged from 6 yr on the southwest Grand Bank to 8 yr in the Gulf of St. Lawrence.

Length at M_{50} ranged from 40 cm in the Gulf of St. Lawrence to 50 cm in the Northeast Newfoundland Shelf and Hawke Channel area, with 44 cm being the length at M_{50} for both intermediate areas. Mature females first occurred at 34 cm in the Gulf of St. Lawrence and 40 cm in the southwest slope of the Grand Bank (Fig. 10). Immature fish did not appear in length frequencies beyond 51 cm for southwest Grand Bank and 57 cm for Northeast Newfoundland Shelf–Hawke Channel area.

Discussion

DISTRIBUTION

Research cruises by the *A.T. Cameron* and the Soviet exploratory vessel *Neptun* indicated that Hamilton Inlet Bank is the northern limit of witch flounder distribution. In March 1965, the *Neptun*, while investigating the continental slope, discovered large spawning concentrations near Hawke Channel (Pechenik and Troyanovskii 1970) at depths of 500–700 m. Similar concentrations were reported by the *A.T. Cameron* in area Q-16 (Fig. 3) in April of the following year (Templeman 1966). According to Pechenik and Troyanovskii (1970), witch flounder form prespawning accumulations on the slope of Hamilton Inlet Bank at depths of 500–700 m and along the Northeast Newfoundland Shelf. After spawning they probably disperse and migrate to the edge of the continental shelf.

Stewart (1956), while doing experimental fishing with Danish seine, found the largest concentrations of witch flounder to be on the southwest slope of the Grand Bank with substantial numbers being found on St. Pierre Bank and extending into Fortune Bay. Stewart (1956) found concentrations in the centre of Fortune Bay large enough to support a Danish seine fishery for witch flounder in the early 1950s. However, recent surveys of the St. John's Biological Station indicate the stock size in this area is now well below commercial levels.

Witch flounder have been reported south to the latitude of Delaware Bay (39°N) and prefer the gullies where the bottom is usually of clay, muddy sand, or pure mud, rather than the hard tops of the banks and inshore ground (McKenzie 1955). In summer they generally move up onto the soft mud and in winter go down into deeper gullies (McKenzie 1955). This was also documented by Powles and Kohler (1970) in studying depth distribution of witch flounder on the Scotian Shelf and Gulf of St. Lawrence. They found that in winter, adults were caught off Nova Scotia only in deep holes, the main stocks migrating into deeper water. They also suggested seasonal movements from the Gulf of St. Lawrence to the Scotian Shelf in winter and back in summer. However, Bigelow and Schroeder (1953) found that when witch flounder settled to the bottom fully metamorphosed in the Gulf of Maine they appeared to be more stationary than most flounders and are caught the year round without evidence that they make seasonal movements. Molander (1925) found seasonal movements of witch flounder in Swedish waters similar to that hypothesized by Powles and Kohler (1970) for the Gulf of St. Lawrence. Possibly movements

in and out of the Gulf of St. Lawrence are due to hydrographic changes caused by the coverage of the Gulf area by arctic ice in the winter and its regression in the summer. It is also possible, however, that the results reported in Powles and Kohler (1970) do not indicate movements as much as they indicate seasonal increase and decrease in availability with fish becoming more concentrated in certain areas at various times of the year.

Witch flounder is generally a deepwater species. Goode and Bean (1895) reported catches in 1569 m off southern Nova Scotia, in 1441 m off Chesapeake Bay, and 1100 m off North Carolina. According to the data presented here and commercial trawler records, the optimum depth for fishing witch flounder is 185–366 m. Bigelow and Schroeder (1953) found the optimum depth range to be 110–275 m in the Gulf of Maine area and Molander (1925) found that for Swedish waters it was 145–275 m, both somewhat shallower than reported in this study. A possible explanation for these differences is that cold temperatures in the upper layers in the study area force witch flounder into deeper, warmer waters; however, there is no real evidence to support this.

One of the major gaps in studying the distribution of this species was the location of juvenile fish, particularly in ICNAF Subareas 2 and 3. The only area where they have been reported is along the south coast of Newfoundland (Squires 1961) when catches were made during exploratory cruises for shrimp. Powles and Kohler (1970) reported fair catches of juvenile witch flounder in the northern part of the Esquiman Channel (ICNAF Division 4R) at depths of 183–256 m. The latter area could be a possible source of recruitment for Subareas 2 and 3. Research cruises by ships of the St. John's Biological Station on the Grand and St. Pierre Banks and northward to Funk Island Deep and Hawke Channel have not produced substantial numbers of small fish.

Age and Growth

The difference in growth rate between males and females is probably the result of genetics that determines the physiology and behavior of the fish rather than the result of the environment, because presumably the males and females are subjected to the same set of environmental factors. Because males mature much earlier than females, energy is probably diverted to the formation of sex products, resulting in less energy being available for growth.

One of the most important factors affecting the growth of fishes is food supply, for only if food is available in sufficient quantity and quality can fish attain their maximum growth possible for existing environmental conditions. Temperature also indirectly determines the feeding habits of the fishes because it affects the availability of food. Kohler (1964) and McKenzie (1934, 1935) found that for cod, temperature affected the amount of growth inasmuch as it controlled the food intake of the fish. Other environmental factors, such as density-dependence and abundance of competing species, also have an effect on the rates of growth. Pitt (1975) showed an increase in the growth of American plaice on the Grand Bank to be a result of either a reduction in the number of plaice, a reduction in a competing species such as haddock, or a combination of both. These and other factors may be in effect in certain localities and not in others which would account for growth pattern inconsistencies between areas. Fleming (1960) and Pitt (1967) indicated that for cod and American plaice there was an increase in the growth rate going from north to south and found positive association between the growth rates and temperatures. In contrast to this, witch flounder indicated decreasing size at age from north to south (Fig. 6). At depths where witch flounder are found, temperatures are normally relatively stable from year to year and would not be expected to have much influence on the growth rate, suggesting that one or more other factors mentioned cause the differences.

Witch flounder are generally associated with redfish (*Sebastes marinus*) (McKenzie 1955) and have a similar food spectrum. Because the Gulf of St. Lawrence has a relatively large stock of redfish (from catch records) and the growth rate of witch flounder is slowest in the Gulf of St. Lawrence, competition for food could be a contributing factor (see Brown 1957).

One major problem in relating growth to environmental conditions is the possibility of fish moving from one locality to another either seasonally or just randomly. If this is the case for other areas as has been suggested by Powles and Kohler (1970) for the Gulf of St. Lawrence witch flounder, then a more complicated set of environmental conditions could affect growth. Until more information on movements of this species is available, little else can be stated on the subject of growth patterns.

Sexual Maturity

Molander (1925), in studying plaice and flounder in the Baltic, found that with increased growth rate, maturity appeared at a lower age but at a greater length, implying that the age at

maturity was higher when growth rate was poor. This was also found to be the case for witch flounder of the Newfoundland area. Pitt (1975) indicated for American plaice that faster-growing fish matured at an earlier age but all matured at approximately the same size. This was true also of witch flounder. Males matured at lengths of M_{50} = 25–30 cm and females M_{50} = 40–50 cm with no significant differences between areas, indicating that sexual maturity is probably dependent on size and indirectly on the growth rate rather than age. Alm (1959) says that "with an initially good growth rate maturity is reached at an earlier age than with beginning poor growth rate." The metabolic processes are probably relatively fast with good growth rate. Consequently, differentiation processes in the gonads and maturity apparently occur much earlier, the opposite being the result of poor growth rate. Even though results here agree closely with the suggestions of Alm (1959), exceptions have been found such as that of Fleming (1960) and Pinhorn (1966) for cod. This would seem to indicate that size may not in fact be the crucial factor involved in the onset of sexual maturity.

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Influence of Bovine Growth Hormone and L-Thyroxine on Growth, Muscle Composition, and Histological Structure of the Gonads, Thyroid, Pancreas, and Pituitary of Coho Salmon (*Oncorhynchus kisutch*)

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Groups of underyearling coho salmon (*Oncorhynchus kisutch*) were acclimated to 10 C well water and a photoperiod of 12 h L: 12 h D. Excess ration (Oregon Moist Pellet) was presented daily. Doses of bovine growth hormone (5, 10, 20, 30, or 90 μg bGH/g body wt) and L-thyroxine (0.5, 5, or 30 μg T_4/g) were administered over a period of 84 days (phase I) either by injection (via dorsal musculature or peritoneal cavity) or by hormone cholesterol implants into the muscle. Administration frequency of bGH and T_4 was such (range 2 times/wk–1 time/3 wk) that fish theoretically received either 10 or 30 μg bGH/g per wk or 1 or 10 μg T_4/g per wk. Control fish received either alkaline saline (pH 9.5) or a cholesterol pellet. After cessation of treatment the fish were observed for an additional 84 days (phase II). During phase I, growth rates (weight) for bGH fish (2.0–2.4% per day) and for T_4 fish (0.97–1.1% per day) were significantly higher than those of control fish (0.42–0.59% per day). Among bGH fish, dorsal musculature injection (2 times/wk) was significantly more effective than intraperitoneal injection (1 time/2 wk).

Increases in weight above control for bGH fish at 84 days ranged from 220 to 369%. Those for T_4 fish extended from 47 to 78%. In phase II, control fish growth rates were higher (0.61–0.67% per day) than those for bGH fish (0.47–0.57% per day) and T_4 fish (0.32–0.44% per day). Administration of bGH and T_4 (high dose) caused a progressive decline in condition factor of fish from the control range. This trend was stopped and reversed in phase II.

At 84 days, generally no significant differences were detected among groups for percentages of muscle water. However, some groups had significantly higher (bGH) and others lower (T_4) percentages of muscle protein relative to those of control fish. Also, significant increases (T_4) and decreases (bGH) in muscle lipid percentages were found. Hormone treatment altered the histological structure of the ovary, thyroid, exocrine (T_4) and endocrine (bGH) pancreas, and somatotrop cells (T_4) of the pituitary. A poor growth response was noted for two groups of coho administered bGH after acclimation to sea water.

HIGGS, D. A., E. M. DONALDSON, H. M. DYE, AND J. R. MCBRIDE. 1976. Influence of bovine growth hormone and L-thyroxine on growth, muscle composition, and histological structure of the gonads, thyroid, pancreas, and pituitary of coho salmon (*Oncorhynchus kisutch*). J. Fish. Res. Board Can. 33: 1585–1603.

Nous avons acclimaté des groupes de saumons coho (*Oncorhynchus kisutch*) de moins d'un an à de l'eau de puits à 10 C et à une photopériode de 12 h d'éclairage et 12 h de noirceur. Nous leur avons offert quotidiennement une ration en excès (boulettes humides d'Orégon). Nous leur avons administré des doses d'hormone de croissance bovine (5, 10, 20, 30 ou 90 μg HCb/g de poids corporel) et de L-thyroxine (0.5, 5 ou 30 μg T_4/g) sur une période de 84 jours (phase I) soit par injection (via la musculature dorsale ou la cavité péritonéale) soit par hormone: implantation de cholestérol dans le muscle. La fréquence d'administration de HCb et de T_4 était telle (variant de 2 fois/semaine à 1 fois/3 semaines) que les poissons recevaient théoriquement soit 10 ou 30 μg HCb/g par semaine, ou 1 ou 10 μg T_4/g par semaine. Les poissons témoins reçurent soit une saline alcaline (pH 9.5) soit une boulette de cholestérol. Nous avons observé les poissons durant une période supplémentaire de 84 jours (phase II) après la fin du traitement. Pendant la phase I, les taux de croissance (poids) des poissons traités à la HCb (2.0–2.4% par jour) et des poissons traités à la T_4 (0.97–1.1% par jour) sont nettement plus élevés que ceux des témoins (0.42–0.59% par jour). Chez les poissons traités à la HCb, l'injection de la musculature dorsale (2 fois/semaine) est significativement plus efficace que l'injection intrapéritonéale (1 fois/2 semaines). L'augmentation du poids des poissons traités à la HCb est de 220 à 369% de celle des témoins après 84 jours. Celle des poissons traités à la T_4 se situe entre 47 et 78%. Pendant la phase II, les taux de croissance des témoins sont plus élevés (0.61–0.67% par jour) que ceux des poissons

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traités à la HCb (0.47–0.57% par jour) et des poissons traités à la T_4 (0.32–0.44% par jour). L'administration de HCb et de T_4 (dose élevée) cause un déclin progressif de l'état d'embonpoint des poissons par rapport à la gamme des témoins. Cette tendance s'arrête et prend une direction inverse durant la phase II.

A 84 jours, nous ne détectons pas en général de différences significatives parmi les groupes dans les pourcentages d'eau du muscle. Cependant, certains groupes montrent des pourcentages de protéines musculaires nettement plus élevés (HCb) et d'autres plus bas (T_4) que ceux des témoins. Nous avons également observé des augmentations (T_4) et des diminutions (HCb) dans les pourcentages de lipides du muscle. Le traitement hormonal change la structure histologique de l'ovaire, de la thyroïde, du pancréas exocrine (T_4) et endocrine (HCb) et des cellules somatotropes (T_4) de l'hypophyse. Nous avons noté une réponse de croissance ralentie chez deux groupes de saumons coho traités à la HCb après acclimatation à l'eau de mer.

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BOTH fish and mammalian growth hormones (reviews: Pickford and Atz 1957; Pickford 1959; Ball 1969; Chester Jones et al. 1974) and thyroid hormones (reviews: Pickford and Atz 1957; Dodd and Matty 1964; Gorbman 1969) can influence fish growth either directly or indirectly. Studies concerned with the influence of mammalian pituitary extracts or hormones on salmonid growth have been conducted on all three genera, namely, *Salvelinus* (Cantilo and Regalado 1942), *Salmo* (Swift 1954; Chartier-Baraduc 1959; Enomoto 1964), and *Oncorhynchus* (Higgs et al. 1975). The studies on *Salmo* and *Oncorhynchus* were preliminary in design and were conducted on fish that were at least 1 yr old. Effects of thyroid hormones on fish growth have been inconsistent (Gorbman 1969) and may largely be dependent upon experimental conditions (Barrington et al. 1961; Narayansingh and Eales 1975).

Previously, we reported that doses of 10 and 100 μg bovine growth hormone (bGH)/g per wk administered to yearling intact coho salmon (*Oncorhynchus kisutch*) by intraperitoneal injection (3 times/wk) or by pellet implantation (1 time/2 wk) were equipotent in enhancing growth at 10 C. Method of hormone administration did not significantly influence the growth response of bGH fish. However, the hormone administration procedures were time consuming and not practical for treatment of large numbers of fish. In addition, implantation of pellets into the peritoneal cavity led to high mortality due to stress from spreading infection around the incision sites.

Therefore the main objective of the present study was to develop more practical (economical) and less stressful means of hormone administration. Our approach was first to extend the interval between bGH injections hoping to maintain the maximum growth response to bGH. Through concomitant manipulation of dosage, the coho were provided with an amount of bGH known to be effective in promoting growth (10 μg/g per wk). Second, we attempted to improve the pellet procedure developed in the previous study to obtain slow release of hormone. Because there is still some controversy concerning the effects of thyroid hormone on fish growth, we assessed the potential of L-thyroxine (T_4) to promote underyearling coho salmon growth at 10 C. There is no information in the literature concerning what effect prolonged bGH treatment has on the ability of salmon to survive transfer to sea water. Also, nothing is known about how such fish would respond to hormone treatment in sea water. Hence, this was studied. Since we used underyearling instead of yearling coho salmon for the present study, we once again investigated the effects of bGH on muscle composition and condition factor or weight–length relationship. This was also done for T_4. In this study we included for histological examination not only the thyroid and gonads of control and treated fish but also the pituitary and pancreas, hoping to gain some insight into the possible hormone interactions on fish growth.

Ultimately, we hope that knowledge of hormonal mechanisms and procedures for manipulating salmon growth will be applicable to the culture of Pacific salmon either for resource enhancement or aquaculture.

Materials and Methods

In July 1974, underyearling coho salmon (*O. kisutch*) weighing between 4.42 and 8.54 g (1 SD limits of population mean) were randomly distributed to 15 tanks ($n = 65$ fish per tank). Experimental conditions such as photoperiod, water temperature, ration, etc. were identical to those used by Higgs et al. (1975). All groups of fish were acclimated to these conditions for 42 days prior to initiation of hormone treatment. Both ration and hormone dosage were adjusted according to the new mean fish weight in each tank at every 14-day interval.

HORMONE ADMINISTRATION

Bovine growth hormone (National Institute of Arthritis Metabolism and Digestive Diseases, NIH-

GH-B-17 [0.92 IU/mg]) and Na-L-thyroxine pentahydrate (Sigma Chemical Co., St. Louis, Mo.) were either injected or implanted as a hormone cholesterol pellet. Details of the thyrotrophin, luteinizing hormone and follicle-stimulating hormone contamination of NIH-GH-B-17 as well as the prolactin activity of this preparation have been provided by Higgs et al. (1975).

Injection of bGH was either intraperitoneal (i.p.) or intramuscular (i.m.); T_4 was injected only via the latter route. The i.p. site was directly in front of the pelvic fins, while the i.m. site was midway between the lateral line and dorsal fin. For i.m. injection both sides of the fish were used. Adminstration frequencies and doses of bGH and T_4 for each group of coho salmon have been included in Table 1. T_4 doses refer to the free acid. On an injection day, lyophilized bGH was dissolved by following the procedure of Clarke (1973), except 0.7% NaCl was used as saline. The pH of all bGH and control solutions was adjusted to 9.5 with NaOH. The lower dose of T_4 was dissolved in a similar manner to that for bGH, but the higher dose of T_4 was dissolved by adding 1 N NaOH so that the final pH of the solution was close to 11. Volume of injection vehicle for all fish was 50 μl, delivered from a 2.5-ml gas-tight Hamilton syringe (Model 1002), with a PB600-1 repeating dispenser. The syringe was affixed with a 27-gauge, 1.3-cm disposable needle.

Pellets (p.) were manufactured by following the procedure of Higgs et al. (1975). Table 1 contains details of administration frequency and doses for both bGH and T_4 pellets for each experimental group. The percentage hormone by weight depended upon the dosage. Lower dose bGH pellets and T_4 pellets contained 3.3–9.0% hormone during the course of the experiment. Higher dose bGH pellets ranged from 9.0 to 27% hormone. Increasing the percentage of hormone was necessary to reduce the size of the pellets implanted into the fish at 42 and 63 days. Pellets for control fish were composed of cholesterol only. Their size was equal to that of experimental pellets (0.033–0.1% body wt).

The following procedure was used to implant pellets into the dorsal muscle of anesthetized fish. First, a small incision was made midway between the lateral line and dorsal fin. Then a tunnel was made into the muscle using a 2-mm diam stainless steel trocar. By using a pair of forceps and then a fire polished glass rod, the pellet was pushed to the end of the channel. Finally, one drop of Terramycin® (50 mg/ml) from a 27-gauge needle, followed by a drop of Eastman 910 adhesive (Eastman Kodak Co.) was applied to the wound. A total of four pellets were implanted alternately on the right and left sides of the fish.

Muscle Analysis

Six fish were removed from each tank at 28, 56, and 84 days for determination of muscle water, lipid, and protein content. All procedures have been described by Higgs et al. (1975).

Histological Techniques

Fish from representative treatment groups (Table 3) were sampled at 84 days. Each was killed by severing the spinal cord, just caudal to the head. Samples of the gonad, the subpharyngeal area (containing the thyroid follicles), the pituitary gland, and portions of the pyloric ceca (containing the pancreas) were excised and fixed in Bouin–Hollande sublimate, processed, and embedded in Paraplast, mp 56 C. Sections 5-μm thick were stained with Mayer's hematoxylin and eosin (H & E), Masson's trichrome, and periodic acid Schiff (Culling 1974). To enable differentiation between α and β cells in the islets of Langerhans, sections of the pancreas were stained with Gomori's aldehyde fuchsin (A.F.) (Pearse 1961). An index of thyroid activity was obtained for each fish by measuring the epithelial height at five separate locations in five randomly selected follicles.

Experiment 2

This experiment was designed to assess if fish previously treated with bGH over a prolonged period in freshwater could survive transfer to sea water and if so still respond to bGH treatment.

On day 173 of the experiment the remaining control fish in groups 2 and 4 (Table 1) were pooled and then randomly and equally distributed to two tanks. A similar procedure was followed for bGH-treated fish in groups 3 and 5. All groups of fish were held in running 10 C well water under a natural photoperiod for 21 days. Excess ration was presented daily.

Acclimation to sea water was conducted in several steps (¼, ½, ¾, and all sea water) over 12 days. The details of bGH treatment of these fish can be found in Table 5. Fish were weighed and measured every 14 days from the beginning of bGH administration for a period of 70 days. Ration and hormone dosage were adjusted as in experiment 1. During the experiment, sea water temperature ranged from 6–9 C and salinity varied between 25.6 and 29.8‰.

Data Analysis

Mean weights (Fig. 1) or lengths (Fig. 2) increased in an exponential manner for all groups of fish. Therefore, regression equations were computed for each treatment group (Table 1) for phase I, the period of hormone treatment (0–84 days), and for phase II, the period when no hormone was administered (84–168 days).

The condition factor, a, which relates fork length (L) to body weight (W) and hence is an index of the fatness or leanness of fish was calculated as follows:

$$a = \frac{W(g)}{L(cm)^{3.25}} \times 1000$$

The value 3.25 was determined for juvenile coho salmon by Vanstone and Markert (1968).

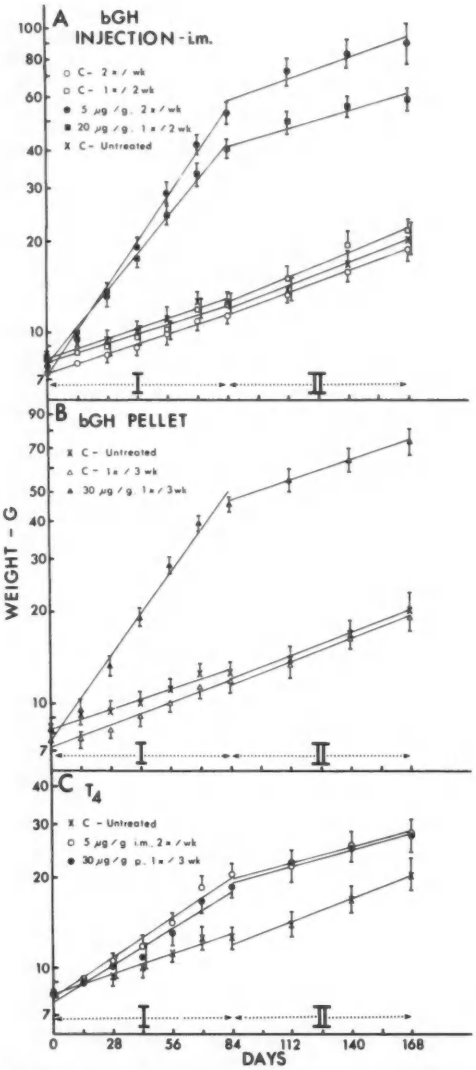


FIG. 1. Semilogarithmic plot of geometric means for wet weights of representative groups of underyearling coho salmon (*Oncorhynchus kisutch*) administered either bGH (A, B) or T_4 (C). |, through the geometric means denote 95% confidence intervals. Administration of the hormones in Phase I (0–84 days) was by dorsal musculature injection or implantation of a hormone cholesterol pellet. Control (C) fish received alkaline saline or a cholesterol pellet. Hormone treatment was stopped in phase II (84–168 days). Each point is a mean of 40–65 fish in phase I and 16–44 fish in phase II.

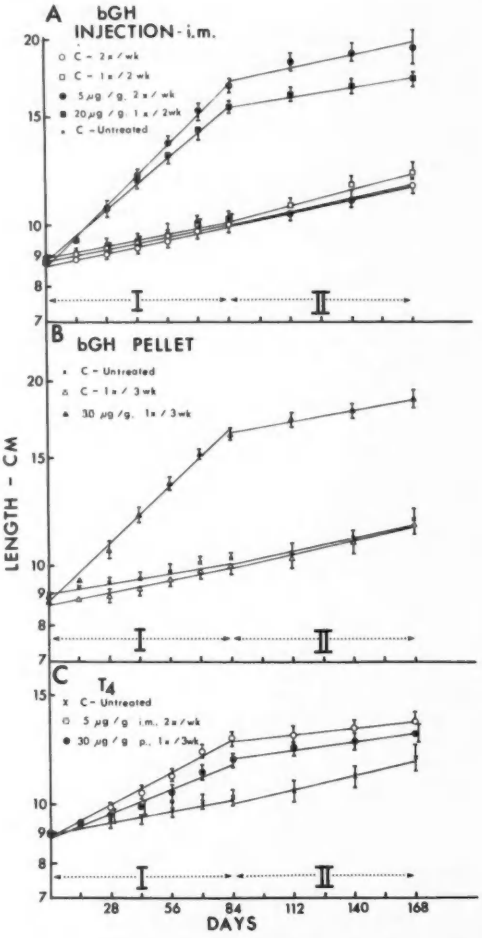


FIG. 2. Semilogarithmic plot of geometric means for fork lengths of representative groups of underyearling coho salmon administered either bGH (A, B) or T_4 (C). |, through the geometric means denote 95% confidence intervals. Refer to Fig. 1 for details.

Results

EXPERIMENT 1

Weight and length increase — In phase I, groups of fish administered bGH (bGH fish) or T_4 (T_4 fish) had greater increases in weight (Fig. 1 and Table 1) and length (Fig. 2 and Table 1) than those groups of fish receiving solvent or cholesterol pellets (control fish).

Growth rates (Table 1) for bGH fish ranged

TABLE 1. Percent increases in weight and length above control of coho salmon (*Oncorhynchus kisutch*) at 84 days and equations for the linear regressions for $\log_e$ of weight (grams) or length (centimeters) against time (days) for phases I and II of experiment 1. Hormone was administered in phase I (0–84 days) while no hormone was supplied in phase II (84–168 days). Multiplying the slope b of the regression by 100 provides the specific growth rate (percent per day).

Group	Treatment[a]					Weight (g) $\log_e y = a + bX$				Length (cm) $\log_e y = a + bX$				% above control at 84 days	
						Phase I		Phase II		Phase I		Phase II			
	Hormone	Route	Dose (μg/g)	Frequency	Dose/wk (μg/g per wk)	a	b	a	b	a	b	a	b	Weight	Length
1	C	—	—	—	—	2.128	0.00504	1.951	0.00628	2.196	0.00155	2.150	0.00185	—	—
2	C	i.p.	—	2/wk	—	2.005	0.00467	1.821	0.00660	2.168	0.00144	2.108	0.00207	—	—
3	bGH	i.p.	5	2/wk	10	1.974	0.0232	3.523	0.00493	2.153	0.00782	2.698	0.00144	345.6	67.3
4	C	i.m.	—	2/wk	—	1.993	0.00526	1.908	0.00613	2.160	0.00166	2.135	0.00192	—	—
5	bGH	i.m.	5	2/wk	10	1.969	0.0242	3.590	0.00566	2.153	0.00806	2.723	0.00158	368.6	69.0
6[b]	C	i.m.	—	1/wk	—	2.097	0.00423	—	—	2.189	0.00140	—	—	—	—
7	bGH	i.m.	10	1/wk	10	2.067	0.0209	3.352	0.00519	2.175	0.00707	2.640	0.00147	245.8	54.4
8	C	i.m.	—	1/2 wk	—	2.077	0.00513	1.972	0.00668	2.179	0.00168	2.136	0.00222	—	—
9	bGH	i.m.	20	1/2 wk	10	2.053	0.0200	3.326	0.00471	2.171	0.00696	2.635	0.00134	220.0	52.4
10	C	p.	—	1/3 wk	—	1.976	0.00588	1.904	0.00636	2.153	0.00174	2.112	0.00206	—	—
11	bGH	p.	30	1/3 wk	10	2.027	0.0224	3.375	0.00553	2.164	0.00777	2.681	0.00147	282.0	64.0
12	bGH	p.	90	1/3 wk	30	1.872	0.0229	3.251	0.00567	2.112	0.00787	2.645	0.00140	247.5	59.0
13	T_4	i.m.	0.5	2/wk	1	2.013	0.00973	2.545	0.00321	2.166	0.00294	2.325	0.00103	46.6	12.0
14	T_4	i.m.	5	2/wk	10	2.079	0.0109	2.632	0.00420	2.177	0.00432	2.461	0.00088	78.0	28.0
15	T_4	p.	30	1/3 wk	10	2.050	0.0100	2.588	0.00437	2.173	0.00330	2.373	0.00116	59.8	18.0

[a] C = control; bGH = bovine growth hormone, NIH-GH-B17 (0.92 IU/mg); T_4 = L-thyroxine; i.p. = intraperitoneal; i.m. = intramuscular; p. = pellet.
[b] On day 51 of the experiment 43% of the fish in this group were accidently killed.

from 2.0 to 2.4% wt per day or from 0.70 to 0.81% length per day. The range in growth rate of T_4 fish was lower than observed for bGH fish both for weight (0.97–1.1% per day) and length (0.29–0.43% per day). Values for growth rates of control fish did not exceed 0.6% wt per day, while those for length were not above 0.18% per day.

The sequence for growth rate (weight) within bGH groups (Table 1) was as follows: group 5 (5 μg/g, 2 times/wk i.m.) > group 3 (5 μg/g, 2 times/wk i.p.) > group 12 (90 μg/g, 1 time/3 wk p.) > group 11 (30 μg/g, 1 time/3 wk p.) > group 7 (10μg/g, 1 time/wk i.m.) > group 9 (20 μg/g, 1 time/2 wk i.m.) > control groups. For T_4 groups the order was: group 14 (5 μg/g, 2 times/wk i.m.) > group 15 (30 μg/g, 1 time/3 wk p.) >group 13 (0.5 μg/g, 2 times/wk i.m.) > control groups. Subsequent descriptions of hormone-treated groups in the text include only hormone dosage and route of administration.

A test of common slope (U.B.C. SLTEST) for $\log_e$ weight revealed significant differences among the 15 groups ($P < 0.001$). Scheffé's test ($P = 0.05$) then showed that the rate of increase in weight for all bGH groups was significantly greater than that of T_4 and control groups. Among bGH groups, i.m. injections twice per week resulted in a slope that was significantly greater than that noted following i.m. injection once every 2 wk. All other comparisons were not significant. The slopes for T_4 groups were not significantly different from one another, but were significantly greater than those of respective control groups. No differences were detected among the slopes of control groups. The results of a test of common slope for $\log_e$ length and Scheffé's test were the same as for $\log_e$ weight except that the slope of group 14 (T_4 5 μg/g i.m.) (Table 1) was significantly greater than that of group 13 (T_4 0.5 μg/g i.m.).

An unbalanced analysis of variance (ANOVA) of $\log_e$ weights or lengths, using a least squares solution (BMD 10V — general linear hypothesis) followed by Student Newman–Keuls test (SNK) with $P = 0.05$, indicated that the weights and lengths of 14 out of 15 groups were homogeneous at the beginning of the experiment. The weights and lengths of only group 12 fish (Table 1) were significantly lower than in some of the other groups. At 14 days some bGH groups (3, 5, 7, and 11; Table 1) and two T_4 groups (14 and 15) had weights that were significantly higher than their respective control groups. By 28 days, weights and lengths of all bGH groups were significantly greater than their appropriate controls. Also, increases in weight and length of most bGH groups were significantly higher than those of T_4 groups. At subsequent times, the differences between bGH and T_4 fish either for weight or length increase became even more pronounced.

Percentage increases in weight (Table 1) above appropriate controls at 84 days ranged from 220 to 369% for bGH fish. In contrast, the range for

T_4 fish was 47–78%. Percentages for length increase of bGH fish (Table 1) ranged from 52 to 69% while those for T_4 fish extended from 12 to 28%.

In phase II, the range in growth rate for weight (Table 1) of control fish (0.61–0.67% per day) was higher than observed for bGH fish (0.47 to 0.57% per day) or T_4 fish (0.32–0.44% per day). This was also true for length (Table 1). However, no significant differences ($P > 0.05$) were found between the slopes for weight of the groups in this phase (test of common slope). As might be expected, because of the rapid growth of hormone-treated fish in phase I relative to that of control fish (Fig. 1) the intercepts were significantly different (test of common equation indicated $P < 0.001$).

Percentage increases in weight and length above control for bGH and T_4 fish at 168 days were in most cases lower than at 84 days.

Condition factor a — Administration of bGH or T_4 (high dose by injection or pellet only) resulted in a continuous decline in mean values of *a* from the control range (Fig. 3). At 84 days, the range in condition factor of control fish was 6.40 (i.m. 2 times/wk) to 6.68 (p. 1 time/3 wk) while that for bGH fish was 5.17 (30 μg/g p.) to 5.51 (10 μg/g i.m.). Values of *a* for T_4 fish extended from 5.24 (5 μg/g i.m.) to 6.56 (0.5 μg/g i.m.) and therefore overlapped the ranges for bGH and control fish. The values of *a* for all bGH groups at this time were significantly lower than those for respective control groups. This was also true for two of the T_4 groups (5 μg/g i.m. and 30 μg/g p.). The value of *a* for the group administered 0.5 μg T_4/g i.m. was not significantly different from that of the control (ANOVA of values of *a* indicated $P < 0.001$; SNK test $P = 0.05$).

Cessation of hormone treatment resulted in a gradual increase in *a* for bGH fish (Fig. 3A, B) and for two groups of T_4 fish (Fig. 3C) toward the control range.

Muscle percentages of protein, lipid, and water — Group percentages (untransformed and arc sine square root transformed) for muscle protein, lipid, and water at 28, 56, 84 days were analyzed (ANOVA and SNK test $P = 0.05$) for significant differences.

Mean percentages of muscle protein for bGH groups at 28 days were significantly lower than those of respective control groups. As a general trend, bGH fish protein percentages slowly increased toward those of control fish between 28 and 84 days. The percentages for groups 9 (20 μg/g i.m.) and 11 (30 μg/g p.) at 84 days were significantly greater than their corresponding control values (Table 2). T_4 treatment did not significantly influence protein percentages except at 84 days. At this time, group 14 (5 μg/g i.m.) had a significantly lower mean percentage of muscle protein than group 4 (control i.m. 2 times/wk).

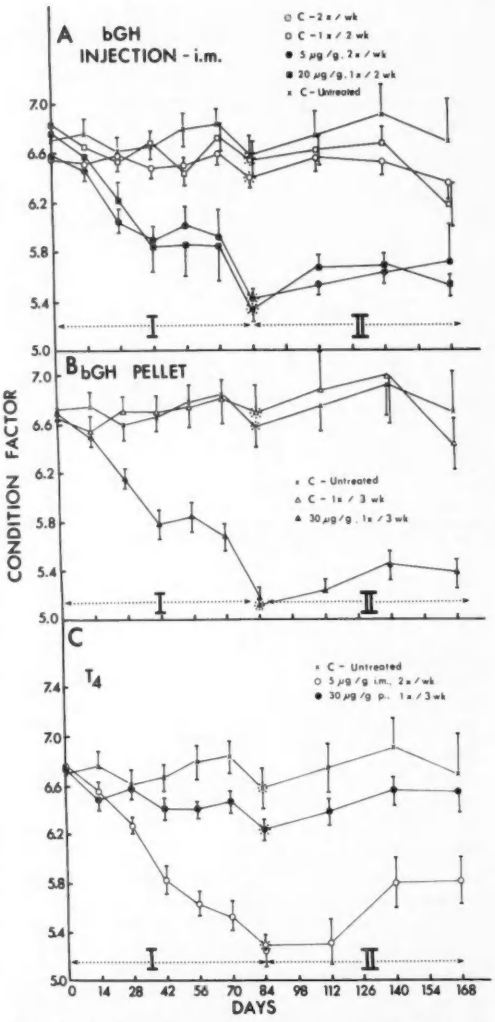


FIG. 3. Mean values ± 2 SE for condition factor of representative groups of underyearling coho salmon administered either bGH (A, B) or T_4 (C). Refer to Fig. 1 for details. Symbols surrounded by (·) show the initial mean condition factors for each of the groups in phase II.

TABLE 2. Mean percentages ± 2 SE of water, protein, and lipid in the muscle of underyearling coho salmon administered bovine growth hormone (bGH) or thyroxine (T_4). Six fish were sampled from each treatment group at 28, 56, and 84 days from the beginning of experiment 1.

Group	Hormone	Route	Dose (μg/g)	Frequency	Water (%)			Protein (%)			Lipid (%)		
					28	56	84	28	56	84	28	56	84
1	C	—	—	—	76.6±0.69	77.3±0.75	77.0±0.76	18.7±0.22	17.9±0.31	18.4±0.22	2.26±0.26	2.84±0.25	2.82±0.22
2	C	i.p.	—	2/wk	76.8±0.66	77.5±0.47	77.2±0.20	18.9±0.23	18.3±0.38	18.6±0.09	2.26±0.21	2.65±0.18	2.59±0.21
3	bGH	i.p.	5	2/wk	79.7±0.35	79.4±0.36	79.2±0.76	16.9±0.25	17.7±0.38	18.2±0.39	2.20±0.14	2.05±0.15	2.19±0.25
4	C	i.m.	—	2/wk	78.6±0.70	77.5±0.68	76.9±1.00	18.6±0.29	17.3±0.47	17.9±0.35	2.22±0.17	2.60±0.29	2.82±0.33
5	bGH	i.m.	5	2/wk	80.6±0.63	81.0±2.07	79.9±1.40	17.0±0.34	17.0±0.66	18.1±0.57	2.12±0.20	2.30±0.17	1.94±0.14
6[a]	C	i.m.	—	1/wk	77.3±1.03	—	—	18.3±0.25	—	—	2.32±0.23	—	—
7	bGH	i.m.	10	1/wk	79.4±0.73	78.7±0.43	78.6±0.44	17.1±0.58	17.3±0.40	18.6±0.51	2.37±0.18	2.38±0.25	2.09±0.24
8	C	i.m.	—	1/2 wk	77.2±0.68	77.2±0.83	77.8±0.54	18.1±0.49	18.4±0.55	18.2±0.32	2.61±0.38	2.45±0.28	2.89±0.29
9	bGH	i.m.	20	1/2 wk	79.3±0.79	79.1±0.29	78.6±0.54	16.8±0.44	17.6±0.25	19.1±0.32	2.48±0.23	2.21±0.17	2.03±0.21
10	C	p.	—	1/3 wk	77.8±1.36	77.4±0.42	77.7±0.47	18.4±0.40	18.4±0.31	17.8±0.53	2.02±0.45	2.80±0.14	2.93±0.31
11	bGH	p.	30	1/3 wk	80.4±0.64	79.3±0.53	78.7±0.16	16.7±0.22	17.6±0.73	19.0±0.34	2.15±0.22	2.35±0.13	2.03±0.17
12	bGH	p.	90	1/3 wk	80.0±0.79	79.8±0.29	77.4±2.28	16.5±0.47	17.1±0.55	18.4±0.40	2.22±0.13	2.22±0.18	2.21±0.12
13	T_4	i.m.	0.5	2/wk	78.0±0.78	77.2±1.14	76.8±0.40	17.9±0.23	16.6±0.41	17.4±0.35	2.60±0.20	3.84±0.77	4.22±0.68
14	T_4	i.m.	5	2/wk	78.3±0.88	78.1±1.04	78.2±1.37	18.0±0.36	16.4±0.59	17.0±0.25	2.75±0.35	3.29±0.76	3.63±0.73
15	T_4	p.	30	1/3 wk	77.0±1.17	77.8±0.62	78.0±1.24	17.9±0.49	17.6±0.30	17.8±0.56	2.57±0.40	3.25±0.36	3.73±0.54

[a]On day 51 of the experiment 43% of the fish in this group were accidentally killed.

Analysis of muscle lipid data at 28 days revealed that group 14 (T_4 5 μg/g i.m.) had a significantly greater percentage of muscle lipid than group 10 (control p 1 times/3 wk). At 56 days, the lipid percentages for T_4 groups had significantly increased above those of bGH groups. Also, two of the T_4 groups (0.5 μg/g i.m. and 30 μg/g p.) had significantly higher lipid percentages relative to their control groups (Table 2). In general, lipid percentages for bGH groups were lower at all sample times than observed for their respective control groups (Table 2). Those for groups 5 (5 μg/g i.m.), 9 (20 μg/g i.m.), and 11 (30 μg/g p.) at 84 days had significantly decreased. In contrast, lipid percentages for T_4 groups at 84 days were significantly higher than found for all other groups.

At 28 days, percentages of muscle water for bGH groups were homogeneous but significantly higher than respective control groups. Only two bGH groups (5 μg/g i.m. and 90 μg/g p.) had greater muscle water percentages than those of controls at 56 days. With one exception, no significant differences could be found between bGH and control groups at 84 days ($P > 0.05$). Percentages for muscle water of T_4 fish were homogeneous at all sample times and equal to those of control fish.

Histology — Gonad — In all groups, the testes consisted of small, ill-defined cysts packed with spermatogonia. Structurally it was clear that no alterations were indicated in any of the hormone-treated fish. Control fish ova (Fig. 4) were in the early perinucleolar stage of development and the egg diameters varied between 120 and 180 μm. T_4 treatment resulted in a mixed response with ova in early and late phases of perinucleolar development. At the lowest dosage of the hormone (0.5 μg/g i.m.) the majority of the eggs appeared to be in the more immature stage with the pallial layer clearly visible. However, in the two groups administered the highest doses of T_4 (5 μg/g i.m. and 30 μg/g p.) the majority of the ova were in the later stage of development. In bGH fish (5 μg/g i.m. and 30 μg/g p.) virtually all of the ova were in the later stage of perinucleolar development. Diameters of the latter varied between 180 and 260 μm (Fig. 5).

Thyroid — In all fish the follicles were concentrated mostly along the areas immediately adjacent to the ventral aorta. Occasionally they were seen scattered throughout the peripheral, loose, connective tissue of the gill region. The thyroid structure of the controls suggested a condition of moderate activity (Fig. 6). The follicle epithelium was low cuboidal and, in general, the nuclei were oriented parallel to the basement membrane. The colloid was evenly distributed, dense, and contained only a few vacuoles located along the periphery. Mitotic figures were only rarely encountered.

Bovine growth hormone administration, in both groups, resulted in changes indicative of increased glandular activity. Not only was there an apparent increase in follicle epithelial height (Table 3), but also, there was a distinct increase in mitotic activity. Most sections contained at least one, and often two or three mitotic figures (Fig. 7). As a rule, the nuclei were large, often indented, and their orientation was perpendicular to the basement membrane. The colloid content was quite variable ranging from dense in a few fol-

TABLE 3. Effect of bovine growth hormone (bGH) and L-thyroxine (T_4) on thyroid follicle epithelial height in normal immature coho salmon from experiment 1. Hormones were administered for 84 days.

Group	Hormone	Route	Dose ($\mu g/g$)	Frequency	No. of fish	Thyroid follicle[a] epithelium ht	*P*
1	C	—	—	—	5	5.33±0.62	
4	C	i.m.	—	2/wk	5	5.11±0.11	
5	bGH	i.m.	5	2/wk	10	6.33±0.29	<0.001
10	C	p.	—	1/3 wk	5	5.25±0.28	
11	bGH	p.	30	1/3 wk	10	6.71±0.56	<0.005
13	T_4	i.m.	0.5	2/wk	5	4.10±0.37	<0.001
14	T_4	i.m.	5	2/wk	10	2.85±0.54	<0.001
15	T_4	p.	30	1/3 wk	10	2.98±0.18	<0.001

[a]Mean value in micrometers ± 2 SE.

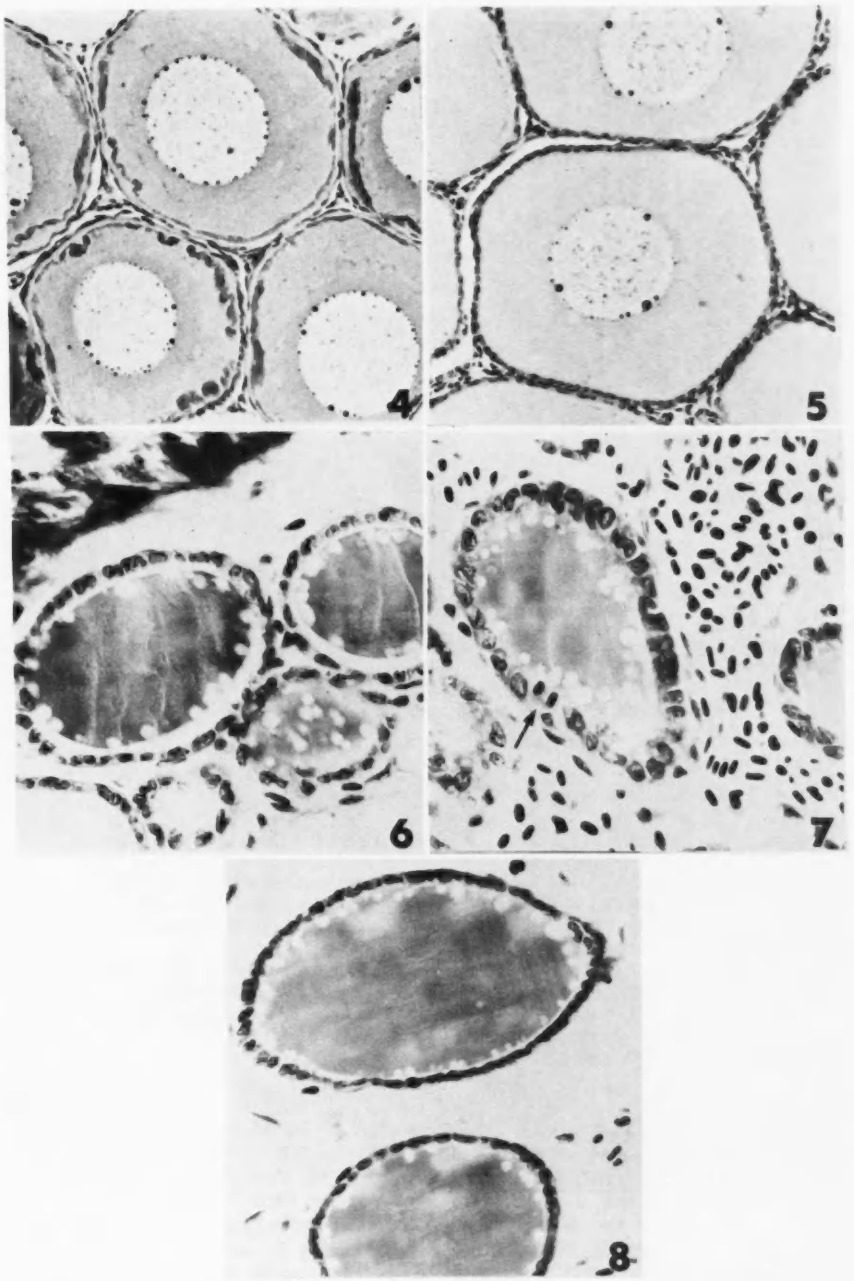
licles to highly vacuolated in others. At the higher doses (5 $\mu g/g$ i.m. and 30 $\mu g/g$ p.), T_4 administration induced alterations which by histological criteria suggested a state of marked suppression. In these fish (Fig. 8), the follicle epithelium height was significantly reduced (Table 3), and the nuclei were flat and oriented parallel to the basement membrane. Their colloid material, however, was not unlike that of the controls. Mitotic activity was not observed. Response to the lowest dosage of T_4 (0.5 $\mu g/g$ i.m.) although significant (Table 3) was not as marked.

Pancreas — In salmon, the pancreas is a diffuse tissue closely associated with the adipose omentum and, ordinarily, distributed in the region of the pyloric ceca. The endocrine portion, the islets of Langerhans, is embedded in the exocrine pancreas. Exocrine cells of control fish were large and, generally, oblong in shape. Their cytoplasm was densely packed with coarse granules. Also, they were characterized by the presence of a basally located round nucleus containing a single conspicuous nucleolus (Fig. 9). The islets were discrete, round to oval in shape, richly vascularized and, generally, ranged in diameter from 10 to 100 μm (Fig. 10). A few large islets measuring 200–300 μm in diameter were noted, but these were the exception. A thin connective tissue capsule enveloped the islets.

Administration of bGH had no apparent effect on the structure of the exocrine portion of the pancreas. In the case of the endocrine component, however, a mixed response was indicated. Of the 20 fish examined, 7 showed no change, but in the remainder the treatment resulted in hyperplasia and hypertrophy (Fig. 11) with several islets attaining a diameter of 400–500 μm. Both α and β cells appeared to be involved and the granulation of the β cells was visibly greater than in the controls (Fig. 11).

T_4 treatment at the lowest dosage had no obvious effect on pancreatic structure. At the high doses the response in the exocrine pancreas was quite variable and most pronounced in those fish that received the hormone by injection. Of the latter, four showed no apparent change, three displayed some degranulation of the cytoplasm while in a further three clear signs of degeneration were noted. In its most pronounced form the degeneration was characterized by marked atrophy of the cells, presence of vacuoles in the cytoplasm, and pyknosis of the nuclei. Such extreme alterations, however, were rare and involved

FIG. 4. Portion of ovary of a control underyearling coho salmon. Ova are in the early perinucleolar stage of development and vary in diameter from 120 to 180 μm. Note presence of dark, irregular granular region of the pallial layer situated close to the follicular layer. H & E × 64; FIG. 5. Ova of an underyearling coho salmon injected for 84 days with bGH (5 $\mu g/g$ i.m.; 2 times/wk). Eggs are in late perinucleolar stage of development. Note absence of pallial layer. H & E × 64; FIG. 6. Thyroid follicles of a control underyearling coho salmon. The follicles contain a generally dense colloid with only a few readsorption vacuoles visible. H & E × 160; FIG. 7. Group of thyroid follicles of an underyearling coho salmon administered bGH (5 $\mu g/g$ i.m.; 2 times/wk) for 84 days. Note the presence of mitotic figure (→). Follicle epithelial height is greater than that of control. H & E × 160; FIG. 8. Thyroid follicles of an underyearling coho salmon injected with T_4 (5 $\mu g/g$ i.m.; 2 times/wk) for 84 days. Histological features indicate a state of marked suppression in activity. Compare with Fig. 6. H & E × 160.



FIGURES 4–8.

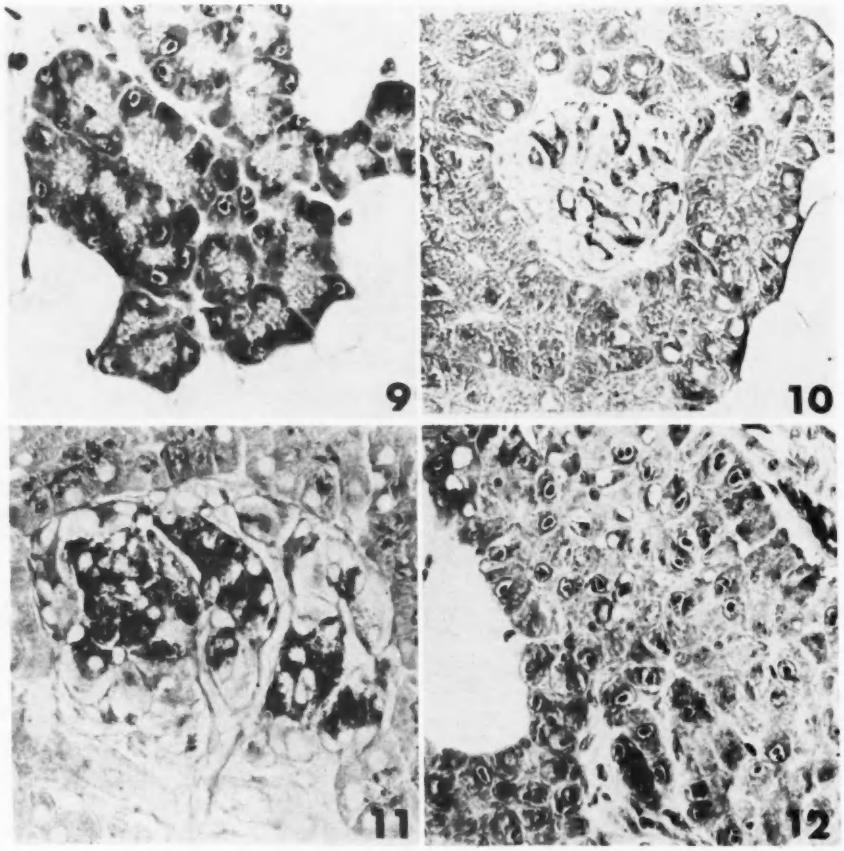


FIG. 9. Exocrine portion of the pancreas of a control underyearling coho salmon. Acinar cells are richly granulated and their nuclei display a single conspicuous nucleolus. Masson's trichrome × 160; FIG. 10. Pancreatic islet of a control underyearling coho salmon showing lightly granulated β cells. Note that the islet is embedded in the exocrine portion of the pancreas. A.F. × 160; FIG. 11. Hypertrophied islet of an underyearling coho salmon injected with bGH (5 μg/g i.m.; 2 times/wk) for 84 days. Note the dense granulation of the β cells. A.F. × 160; FIG. 12. Acinar cells of an underyearling coho salmon injected with T_4 (5 μg/g i.m.; 2 times/wk) for 84 days. Atrophied cells show discrete vacuoles and loss of granulation. Compare with Fig. 9. Masson's trichrome × 160.

only small groups of cells. In its more common form, degeneration involved a general atrophy of the tissue accompanied by degranulation (Fig. 12). Of the pellet-implanted fish, 2 of 10 examined showed a mild atrophy and possibly some degranulation of the exocrine cells. No structural changes were indicated in the endocrine tissue in any of the T_4-treated fish.

Pituitary — The pituitary gland of the control groups reflected the general morphology characteristic of immature salmon.[1] The only variation concerned the differentiation of the basophilic cells. In the majority of the controls these cells were sparse, lightly granulated, and generally only found in the region of the proximal pars distalis

[1]Only an outline noting variation or change is reported. Detailed descriptions of the pituitary zones or areas as well as the cell-types have been published (van Overbeeke and McBride 1967; Chestnut 1970; McKeown and Leatherland 1973).

FIGURE 13.

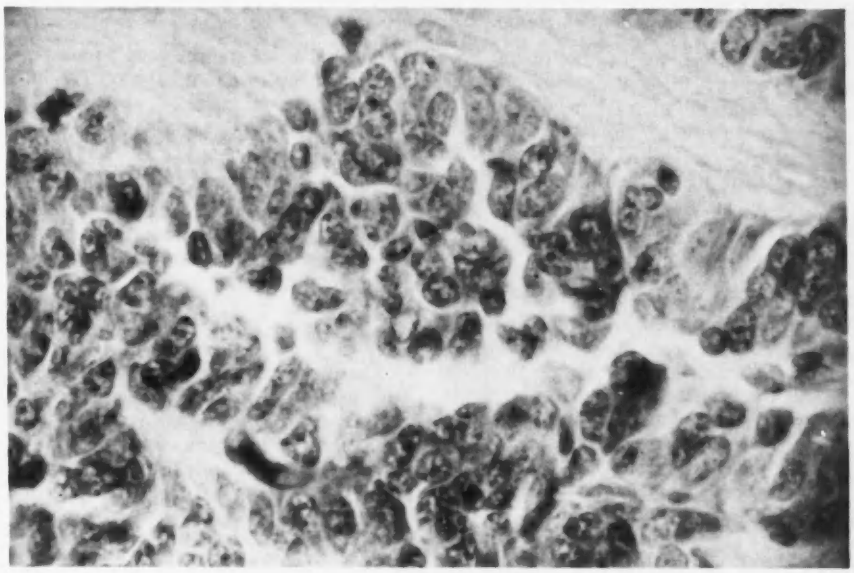


FIGURE 14.

FIG. 13. Portion of proximal pars distalis of a control underyearling coho salmon. The acidophilic cells (→) or somatotrops are the predominant cell type. The basophilic cells which represent gonadotrops or thyrotrops are lightly granulated. Masson's trichrome × 250; FIG. 14. Portion of proximal pars distalis of an underyearling coho salmon administered T_4 (30 μg/g p.; 1 time/3 wk) for 84 days. Somatotrops show degranulation of the cytoplasm. Masson's trichrome × 250.

TABLE 4. Mortality (number of fish that died relative to initial number present for various reasons other than those mentioned below) of experiment 1 coho salmon in phase I, the period of hormone administration (0–84 days) and phase II, the interval when no hormone was supplied (84–168 days). Six fish were removed from each treatment group at 28, 56, 84, and 140 days for proximate analysis. At 84 days 5–10 fish were sampled from selected groups for histology (refer to Table 3) and a few for photography.

	Treatment				Mortality	
Group	Hormone	Route	Dose ($\mu g/g$)	Frequency	Phase I	Phase II
1	C	—	—	—	1/63	0/37
2	C	i.p.	—	2/wk	0/64	0/44
3	bGH	i.p.	5	2/wk	2/65	0/43
4	C	i.m.	—	2/wk	4/65	0/36
5	bGH	i.m.	5	2/wk	2/65	0/33
6[a]	C	i.m.	—	1/wk	28/65	—
7	bGH	i.m.	10	1/wk	4/64	0/40
8	C	i.m.	—	1/2 wk	3/65	0/42
9	bGH	i.m.	20	1/2 wk	5/64	0/38
10	C	p.	—	1/3 wk	4/65	2/36
11	bGH	p.	30	1/3 wk	3/65	0/32
12	bGH	p.	90	1/3 wk	9/65	1/35
13	T_4	i.m.	0.5	2/wk	4/64	0/28
14	T_4	i.m.	5	2/wk	13/65	0/22
15	T_4	p.	30	1/3 wk	3/64	0/31

[a]On day 51 of the experiment 43% of the fish in this group were killed due to an accidental leakage of toxic chemicals from the floor above.

near the ventral projection of the rostral pars distalis. In 6 of the 15 control fish, however, these cells were not only more abundant, but also larger with a more richly granulated cytoplasm. Also, while they were still clearly concentrated in the zone adjacent to the rostral pars distalis, a few cells were noted in the deeper regions of the proximal pars distalis.

Treatment with bGH had little, if any, effect on the pituitary cytology. In 7 of the 10 treated fish, there were substantial numbers of large well-granulated β cells, but their appearance and distribution did not differ from that noted in at least a few of the controls. Of particular interest was the state of the somatotrops. In the controls, these cells, which showed a strong affinity for acid dyes, were the predominant cell type (Fig. 13). While mitotic activity among the somatotrops was a common observation in the controls, such activity was not noted in the treated fish.

The most striking changes were noted in the two groups of fish administered the higher doses of T_4. The somatotrops invariably showed marked degranulation of the cytoplasm and in a majority of the fish these cells had visibly undergone atrophy (Fig. 14). Mitotic activity was not observed. The state of the basophils was not unlike that of the other groups. In a few fish these latter cells were abundant and well granulated while in others, they were sparse, small, and contained few granules. No differences were found between the fish given the lowest dosage of T_4 and the controls.

Mortality — Fish mortality (Table 4) in phase I did not exceed 8% of the initial number in each group except in group 6 (on day 51, 43% of the fish were accidentally killed), group 12 (13.8%), and group 14 (20.0%). Mortality in phase II did not exceed 6% of the initial number present in each group.

EXPERIMENT 2

The sequence for growth rate (Table 5) of the four groups of coho salmon in sea water over a period of 70 days was as follows: group D (enhanced coho from experiment 1 + bGH) > group B (control fish from experiment 1 + bGH) > group C (enhanced fish) > group A (control fish). Percent gains over initial weight at 70 days (Table 5) ranged from 8.8 (group A) to 45.6% (group D).

During this experiment, none of the fish in groups A and B died (Table 5). However, mortality of group C fish was 25% and that of group D fish was 8%.

EXTERNAL APPEARANCE

Fish administered bGH appeared streamlined

TABLE 5. Percent gains over initial weight, specific growth rates (percent weight per day), and mortality of coho salmon in experiment 2. Fish in groups A and B were derived from groups 2 and 4 in experiment 1 (Table 1) while those in groups C and D were from groups 3 and 5. Following transfer of fish to sea water, bovine growth hormone (bGH) was administered to two groups of fish over a period of 70 days.

	Treatment									
Group	Hormone	Route	Dose (μg/g)	Frequency	Dose/wk (μg/g per wk)	Initial mean wt (g) ±2 SE	Final mean wt (g) ±2 SE	% gain over initial wt	Growth rate (%/day)	Mortality
A	—	i.m.	—	1/2 wk	—	22.8±1.68	24.8± 3.24	8.77	0.120	0/26
B	bGH	i.m.	20	1/2 wk	10	25.5±1.67	32.5± 3.04	27.4	0.346	0/26
C	—	i.m.	—	1/2 wk	—	100.3±9.13	122.4±22.3	22.0	0.284	5/25
D	bGH	i.m.	20	1/2 wk	10	98.1±7.79	142.8±15.9	45.6	0.536	2/25

with no evidence of deformities. After 28 days treatment, the dorsal and caudal fin tips became blackened. Parr marks were still prominent at the end of experiment 1, but were fading or not evident at the termination of experiment 2.

Fish receiving T_4 had elongated pectoral, pelvic, and caudal fins. The sides of these fish appeared silver and parr marks were not present. The skulls of T_4 fish were broader and higher than those of control fish. All of these external changes were most pronounced for fish injected with 10 μg T_4/g per wk. Only slight abnormalities in skull structure were noted for fish injected with 1 μg T_4/g per wk.

Discussion

WEIGHT AND LENGTH INCREASE

Bovine growth hormone — Growth rates for underyearling coho salmon administered 10 or 30 μg bGH/g per wk were significantly greater than those of control salmon. Significant gains in weight and length were indicated for most bGH groups after 14 days.

Other studies on the influence of bGH on salmonid growth employed similar doses of bGH to those used in the present study (Swift 1954; Enomoto 1964; Chartier-Baraduc 1959; Higgs et al. 1975). Invariably, bGH was effective in enhancing growth. However, none of these investigations, with the exception of the one by Higgs et al. (1975) exceeded 28 days. In one study (Enomoto 1964), conclusions were based on results from three fish in each treatment group and in another (Swift 1954) no indication of water temperature was provided. Water temperature is known to affect the growth response in length of hypophysectomized *Fundulus* to bGH administration (Pickford 1959).

Higgs et al. (1975) administered bGH for 56 days to coho salmon held under similar conditions to those of the present study. The range for growth rate in weight of their bGH-treated yearling coho (1.3–1.6% per day) compared with that for the underyearling bGH-treated coho in the present study (2.0–2.4% per day) was lower. Control fish growth rates in both studies were similar. This indicates that underyearling coho salmon are able to respond to equivalent bGH doses better than yearlings. Therefore, bGH administration to underyearling coho would yield the greatest gains in growth at the lowest cost.

In our study, there has been some attempt to make bGH administration more practical and less stressful to the fish. These are important considerations if the hormone is to be used in fish culture. One approach, and certainly the most convenient, would have been to incorporate bGH into the diet. However, the oral route of administration was given low priority here because the growth hormone is a protein and hence its activity might be destroyed by digestive enzymes. But this route should not be ignored in future investigations, because Cantilo and Regalado (1942) showed that crude mammalian pituitary extracts given orally to *Salvelinus fontinalis* can enhance growth. Pickford and Atz (1957) suggested that there may only be partial digestion of orally ingested growth hormone in fish prior to its entry into the blood stream.

It is now possible, using the conditions of this experiment, to inject bGH once per week or implant a bGH cholesterol pellet, once every 3 wk into the muscle without any significant reduction in maximum growth response. Even bGH injections once every 2 wk resulted in a significant increase in weight and length over control fish after 4 wk. In previous studies, bGH has been injected either into the peritoneal cavity (Pickford 1954; Swift 1954; Chartier-Baraduc 1959; Higgs et al. 1975) or dorsal muscle (Enomoto 1964). Injection frequency ranged from once per day for *Salmo gairdneri* (Chartier-Baraduc 1959) to once every 4th day for *S. irideus* (Enomoto 1964). The interval between pellet implants used

by Higgs et al. (1975) was 2 wk. There was some indication that i.m. injection of bGH was more effective than i.p. injection in enhancing growth. This was observed at an injection frequency of twice per week. Probably bGH absorption into the bloodstream from muscle is slower than from the peritoneal cavity.

The i.m. pellet procedure of the present study was substantially better than the i.p. pellet procedure as outlined by Higgs et al. (1975). First, it was not as time-consuming. Second, the incidence of infection around the implant site was low. Mortality of pellet-implanted fish in the present study during phase II did not exceed 6% of the initial number of fish, whereas in the previous study it was close to 30%. Some of the mortality of pellet-implanted fish in phase I of this study was due to lack of recovery following anesthesia.

Stopping bGH treatment in phase II led to a decline in growth rates for bGH fish to rates close to those of control fish. However, the growth advantage achieved by bGH fish in phase I was not lost in phase II. The same response was observed in yearling coho salmon (Higgs et al. 1975) and provides evidence that bGH treatment and not some other factor was responsible for enhancing coho salmon growth in phase I.

In experiment 2, bGH administration increased the growth rates of both small control and enhanced coho from experiment 1 even at low temperature (6–9 C). However, the low water temperature and/or salinity (25.6–29.8‰) are the most likely causes of the generally poor growth responses noted for all groups of fish in this experiment. In addition, the photoperiod history of these fish may have been a contributing factor. Both control and enhanced fish were able to tolerate transfer to sea water. Mortality of group C and D fish was either due to lack of recovery from anesthesia at the time of weighing or to the fish jumping out of their tanks.

L-thyroxine — While a dosage of 10 μg T_4/g per wk induced slightly but not significantly better gains in weight and length than 1 μg T_4/g per wk, its administration led to pronounced growth anomalies in skull and fin structure as well as to greater mortality when injected (Table 4). Previous studies have shown that thyroid hormones can radically influence the morphogenesis of other fish (Krockert 1936; Grobstein and Bellamy 1939; La Roche et al. 1950; Hopper 1952; La Roche 1953; Dales and Hoar 1954; Honma and Murakawa 1955; and Lam 1973), and largely to avoid such effects we recommend for future investigations that a dosage of 1 μg T_4/g per wk or less be used for enhancing coho salmon growth at 10 C.

There is considerable controversy in the literature as to whether or not the fish thyroid is essential for normal growth. Generally, administration of antithyroid compounds (Hoar and Bell 1950; Gaiser 1952; Hopper 1952; Vivien and Gaiser 1952; Scott 1953; Smith et al. 1953; Dales and Hoar 1954; Honma and Murakawa 1955, 1957; La Roche et al. 1966; Sage 1967) and radiothyroidectomy (Gross et al. 1963; La Roche et al. 1966; Norris 1969) result in growth retardation. Sometimes the negative effects of either antithyroid compounds or radiothyroidectomy on growth can be abolished by treatment with T_4 (Gaiser 1952; Sage 1967; Norris 1969) which suggests that thyroid hormones are necessary for general growth. However, these types of studies have been criticized on the basis of the toxic effects of the antithyroid compounds themselves and of the possible radiation damage to the fish following administration of large doses of radioiodide.

A few studies have demonstrated that T_4 can promote growth of *S. gairdneri* (Fontaine and Baraduc 1955; Barrington et al. 1961; Norris 1969), *Lepomis cyanellus* (Gross et al. 1963), and *Poecilia reticulata* (Sage 1967). In addition, growth enhancement has been observed following administration of mammalian thyroid powder, minced beef thyroid, or iodinated casein to *S. gairdneri* (Barrington et al. 1961; Fontaine and Baraduc 1955), *P. reticulata* (Hopper 1952; Lam 1973) *Xiphophorus helleri* (Lam 1973) and *S. salar* (Piggins 1962). However, Smith and Everett (1943) and Smith et al. (1953) were not able to show any effect of thyroid hormones on growth of *P. reticulata.* Such negative findings have also been reported by Grobstein and Bellamy (1939) for *Platypoecilus variatus* and *P. maculatus*, by La Roche and Le Blond (1954) for *S. salar*, by Honma and Murakawa (1955) for *O. keta*, and by La Roche (1953) for *Salvelinus fontinalis.*

The causes for such discrepancies in findings can or have been attributed to lack of optimal environmental conditions (Barrington et al. 1961), differences in method of hormone administration (Hopper 1952; Smith et al. 1953) and dosage (Lam 1973; Narayansingh and Eales 1975) and the possible administration of T_4 to fish in the presence of naturally occurring goitrogens and/or when the fish have been on low iodine intakes (La Roche et al. 1966). Additional variables include season of the year and the

possibility that salmonids may respond differently to T_4 treatment at different stages in their life history (Fontaine and Baraduc 1955).

In the present study our fish were in the parr stage prior to initiation of treatment and were held under constant conditions of water temperature and photoperiod. Variation of any of these factors may abolish the observed effects of T_4 on coho salmon growth.

Also, our procedures for hormone administration, namely injection and pellet implantation of relatively high doses of T_4 into the dorsal musculature may have been ideal for demonstrating the potential for T_4 to enhance coho salmon growth. These probably caused a sustained elevation in plasma T_4 concentration above normal circulating levels, which for most fish examined to date does not exceed 1 μg/100 ml plasma (Higgs and Eales 1973). This conclusion is not only based on our success with the pellet procedure but also on data of Higgs and Eales (1976). They observed slower turnover of ^{125}I-labelled T_4 in i.m.-injected *S. fontinalis* relative to heart- and coelom-injected trout. There was evidence of slow release of T_4 from muscle to blood. In addition, Eales (1974) discounted the i.p. injection route for T_4 as being impractical for maintaining any physiological chronic elevation of plasma T_4 in *S. fontinalis* because T_4 turnover in this species is very rapid (Higgs 1974). Most likely rapid turnover of T_4 occurs in *O. kisutch* as well.

Other methods available for administering thyroid hormones, besides those above, include addition of the hormone to the water and mixing T_4 and/or triiodothyronine and desiccated thyroid powder with the food. Eales (1974) has shown that the immersion technique can be employed to significantly increase plasma T_4 concentrations of *S. fontinalis*. But, administering T_4 in water was considered impractical in the present investigation, because we decided to feed excess food daily. This necessitates good water flow. The most practical procedure for fish culture is the oral route. However, this too could have led to negative results. There is strong indication from ^{125}I-labeled T_4 studies conducted on starved *S. fontinalis* (Eales and Sinclair 1974) that T_4 is poorly absorbed into the blood from the gut lumen. Also stomach and intestine homogenates from this same species can deiodinate radiothyroxine (Law and Eales 1973). There is therefore some question as to the form and quantity of thyroid hormone actually entering the blood using this route. In spite of these criticisms, now that the potential for T_4 for enhancing coho salmon growth has been established, experiments should be conducted to determine if inclusion of hormone in the food leads to findings similar to those obtained in the present study.

Condition Factor

Higgs et al. (1975) noted that the condition factor of yearling coho treated with bGH progressively declined from the control range until cessation of treatment. This trend was also observed in underyearling coho salmon of the present study and indicated once again that growth hormone induces greater growth in length than weight. Stopping hormone treatment in phase II resulted in a gradual increase in condition factor toward the control range. The rate of this increase was not as rapid for underyearling coho as observed for yearlings. Possibly, the discrepancy in age of the fish between the two investigations can account for the difference in response. Environmental factors such as temperature and photoperiod were the same in both studies.

Administration of 5 μg T_4/g twice per week by injection brought about a similar decline in condition factor to that observed following bGH treatment. However, implanting T_4 cholesterol pellets containing 30 μg/g once every 3 wk led to condition factors only slightly below the control range. This finding along with the observation that coho given 0.5 μg T_4/g twice per week by injection had condition factors slightly above those of their controls provides additional evidence apart from the growth data for slow release of T_4 from the pellet implants.

Histology

Ovary — Both T_4 and bGH influenced ovarian maturation of underyearling coho salmon held at 10 C and maintained on a 12 h photoperiod.

Because the lowest T_4 dosage did not appreciably stimulate ovarian maturation, it is conceivable that the higher doses exerted a pharmacological effect on the hypothalamo–hypophyseal axis and/or directly on the ovary. In other species of fish, namely *Poecilia reticulata*, *Xiphophorus*, and *Carassius auratus*, T_4 has shown an inhibitory effect on pituitary gonadotropic production as assessed by histological criteria (Sage and Bromage 1970; Hurlburt 1975). Hurlburt (1975) proposed that T_4 stimulates ovarian maturation of *C. auratus* by increasing general metabolism or directly stimulating steroidogenic processes within the ovary. This, she suggests, requires the presence of some gonadotropin. Perhaps T_4 stimulated ovarian maturation of coho salmon in a similar manner.

The effect of bGH on ovarian structure in the present study is in direct contrast to results of Higgs et al. (1975). They were unable to show any effect of bGH on the ovary of coho salmon. Factors such as possible differences in the level of gonadrotropin contamination of the bGH preparations as well as use of different age-classes of fish between the two studies may explain the discrepancy in findings.

Alternatively, the apparent effect of T_4 or bGH on ovarian maturation may simply reflect the size differences which existed between hormone-treated and control fish at 84 days.

Thyroid — Histological assessment of thyroid glands of bGH fish indicated increased glandular activity. The increase in activity may have been caused by thyrotropin contamination of the bGH preparation. Mammalian thyrotropin in combination with fish growth hormone can induce a greater growth response than either of the hormones alone in hypophysectomized male *Fundulus* (Pickford and Atz 1957). Hence, the observed effects of bGH on coho salmon growth in the present study may not have been solely due to bGH. Alternatively, changes in fin pigmentation and condition factor following bGH treatment suggest some advancement to the smolt stage. Increased production of thyroid hormones may occur at this time (discussed by Higgs et al. 1975).

Our results showing suppression of thyroid gland activity following T_4 administration are consistent with the known feedback effects of T_4 on the hypothalamus and pituitary of teleosts. These lead to a decrease in pituitary thyrotrophin secretion (Peter 1971).

Pancreas — Prolonged bGH administration to underyearling coho salmon increased the number and size of the islets of Langerhans and in particular β-cell granulation within the islets, relative to that of the controls. Enhanced insulin synthesis in the β cells may have been in response to one or more of three possible actions of growth hormone.

First, bGH may have inhibited peripheral glucose utilization in coho salmon. This would have led to an elevation in plasma glucose concentration necessitating greater insulin synthesis and release to lower blood glucose. Studies on other fish indicate that hyperglycemia probably occurs only after long-term growth hormone treatment. For example, Matty (1962) found that injection of growth hormone into *Cottus scorpio* every 3rd day for 15 days cause marked hyperglycemia. But hyperglycemia could not be demonstrated for the first 3 days. Enomoto (1964) noted pronounced glycosuria, but not hyperglycemia, 2.5 h after injection of bGH into *Salmo irideus*. Also, McKeown et al. (1975) observed nonsignificant elevations in both plasma glucose and liver glycogen above control levels following injection of ovine growth hormone into *O. nerka* for 3 consecutive days. Both acute and long-term effects of growth hormone on carbohydrate metabolism in man have been noted (Adamson and Cerasi 1975).

Second, mammalian studies provide evidence that growth hormone can act directly on pancreatic β cells. Perhaps this occurred in our study. Possibly, bGH enhanced the activating mechanism of glucose on the β cells (Martin and Gagliardino 1967) or stimulated insulin synthesis (Curry and Bennett 1973).

Third, bGH treatment stimulated directly or indirectly the appetite of coho salmon in our study. Increased food consumption could account for the observed differences between bGH and control fish in the endocrine component of the pancreas.

Both growth hormone and insulin are anabolic hormones. In mammals, insulin is required for the full anabolic effect of growth hormone (Daughaday et al. 1975). Therefore bGH may have been acting in combination with thyroid hormones as suggested above, as well as with insulin to enhance coho salmon growth.

The observed changes in the exocrine pancreas of underyearling coho salmon following chronic administration of the high T_4 doses, especially by injection, are probably due to a pharmacological action of T_4. T_4 may have exerted an abnormal influence on release of pancreatic enzymes which are of major importance in digestion. Stimulation of pancreatic enzyme secretion may have been so severe as to cause general atrophy of the tissue. Mammalian pancreatic β cells can be exhausted and undergo atrophy in a similar manner if they are subjected to marked or prolonged hyperglycemia (Ganong 1973).

Pituitary — There was some evidence that bGH exerted a negative feedback influence on pituitary somatotrops of coho salmon. Mitotic activity among the somatotrops of bGH fish was reduced relative to that of controls. This indicates reduced synthesis of endogenous growth hormone.

In mammals, growth hormone secretion is regulated by such factors as the blood glucose level, exercise, starvation, stress, and the ingestion of a high protein meal. Also, the amino acid arginine stimulates growth hormone production (Schreiber 1974). Of these factors, hyperglycemia

in bGH fish could have had the inhibitory effect on the somatotrops, instead of a direct effect of exogenous bGH.

Somatotrop changes following extended administration of high T_4 doses are suggestive of an effect of T_4 on growth hormone release. Such a conclusion is in accordance with the conclusion of other studies (Sage 1967; Singh 1971; Leatherland and Hyder 1975) that have investigated the influence of thiourea, T_4, or both on fish pituitary somatotrop structure.

Muscle Composition

The percentage of muscle water was significantly increased by bGH treatment for the first 56 days of the experiment. A similar trend was observed by Higgs et al. (1975) for yearling coho salmon. Also, Chartier-Baraduc (1959) found that muscle water content of *S. gairdneri* was higher after bGH treatment. In the present study we extended bGH treatment to 84 days. At this time the differences in water content between bGH and control fish were generally nonsignificant. If one assumes that the percentages of muscle water are representative of those of the whole body, then the mean total dry weights of bGH fish were significantly higher than those of control fish at 84 days. This was also true for T_4 fish.

While bGH fish muscle protein percentages were significantly lower than those of control fish at 28 days such was not the case at 84 days. Here the protein percentages of two bGH groups were significantly higher than control values. At 84 days, the average amount of protein in bGH or T_4 fish was higher than that of control fish. Also, the ratios of protein (grams) to dry body weight (grams) were in every instance higher for bGH fish relative to those of respective controls. But, the protein to dry body weight ratios between T_4 and control fish were not different. Apparently bGH and T_4 exerted a protein anabolic or anticatabolic action in our study. This may be the result of either bGH or T_4 acting alone. However, each hormone may have stimulated endogenous production of other protein anabolic hormones. In this case, a combination of hormones may have been stimulating protein synthesis.

At 28, 56, or 84 days, percentages of muscle lipid were lower for bGH fish relative to those of control fish. At 84 days, the ratios of lipid (grams) to dry body weight (grams) were also lower for bGH fish. Probably, bGH was stimulating fat mobilization. In mammals, growth hormone activates lipase which catalyzes triglyceride hydrolysis. The energy derived from lipid oxidation spares dietary protein for growth (Frye 1967). A similar action of bGH on fat metabolism may occur in coho salmon. At all sample times, T_4-fish lipid percentages were higher than respective controls. Also, ratios of lipid (grams) to dry body weight (grams) were greater for T_4 fish than those of controls at 84 days. The results suggest that increased lipid deposition occurs in muscle of coho salmon following T_4 treatment. However, administration of T_4 doses less than 1 μg/g per wk could lead to a different conclusion. For example, Narayansingh and Eales (1975) found that physiological doses of T_4 had little effect on muscle lipid of both starved and fed *Salvelinus fontinalis*.

Concluding Comments

While individual hormones such as bovine growth hormone, L-thyroxine, and the steroid, 17α-methyltestosterone (Fagerlund and McBride 1975) can enhance salmon growth possibly by increasing appetite and/or food conversion efficiency, little is known of the complex interplay of these, plus other hormones, in growth regulation. Experiments should be conducted designed to investigate the growth promoting effects of different hormone combinations on fish of different ages (sizes) and genetic strains held in various nutritional and environmental states. This type of information will enable proper assessment of the biological feasibility of using hormones to enhance salmon growth.

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Effects of Crude Oil on American Lobster (*Homarus americanus*) Larvae in the Laboratory[1]

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Four-day LC50s for Venezuelan Tia Juana crude oil were 0.86 mg/liter for first-stage larvae of the American lobster (*Homarus americanus*) and 4.9 mg/liter for third- and fourth-stage larvae. The 30-day LC50 was 0.14 mg/liter for larvae starting the test in their first stage. The threshold for retardation of larval development was about the same as the 30-day LC50. Decreased food consumption was demonstrated at 0.19 mg/liter. More "intermediate" larvae developed in oil exposures but no threshold was estimated. The ratio of "safe" to acutely lethal concentrations was about 0.03.

Oil concentrations decreased during exposures; stated values could be multiplied by 0.59 to arrive at conventional average exposures. Stirring and ultrasonic vibration for 30 min dispersed averages of 7.4 and 18% of added oil. This and other techniques apparently dispersed similar components since toxicities were the same when based on measured concentrations. Aged dispersions were also equally toxic on a measured basis. Particles larger than 1.2 μm made up 84–96% of the dispersed oil and were about one-third as toxic as smaller particles and dissolved oil. For the reference toxicant DSS, the 4-day LC50 was 0.72 mg/liter for first-stage larvae indicating that lobster larvae are sensitive. Post-larval lobsters dug significantly more burrows when the substrate contained oil but did not avoid oiled substrate nor was growth or survival affected for substrates containing up to 1740 mg/liter of oil.

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Les CL50 après 4 jours du pétrole brut de Tia Juana, Vénézuéla, sont de 0.86 mg/litre pour des larves de homard américain (*Homarus americanus*) au stade 1 et de 4.9 mg/litre pour des larves aux stades 3 et 4. La CL50 après 30 jours est de 0.14 mg/litre pour les larves soumises aux essais au stade 1. Le seuil de retard au développement larvaire est à peu près le même que la CL50 après 30 jours. Il y a diminution de la consommation de nourriture à 0.19 mg/litre. Des larves à des stades plus « intermédiaires » se développent en présence de pétrole, mais nous n'avons pas estimé de valeurs de seuil. Le rapport des concentrations « sûres » aux concentrations létales en phase aiguë est d'environ 0.03.

Les concentrations de pétrole diminuent au cours de l'exposition; on pourrait multiplier les valeurs données par 0.59 pour en arriver aux expositions moyennes conventionnelles. L'agitation et la vibration aux ultrasons pendant 30 mn causent une dispersion des moyennes de 7.4 et 18% du pétrole ajouté. Cette méthode, ainsi que d'autres, semble disperser les composants semblables, puisque les toxicités sont les mêmes lorsque fondées sur des concentrations mesurées. Les dispersions âgées sont également toxiques sur base mesurée. Les particules plus grosses que 1.2 μm constituent jusqu'à 84–96% du pétrole dispersé et ont une toxicité d'environ un tiers de celle des particules plus petites et du pétrole dissous. La CL50 après 4 jours du toxique étalon DSS est de 0.72 mg/litre pour les larves au stade 1, ce qui indique que les larves de homard sont sensibles. Les homards postlarvaires creusent nettement plus de trous quand le substrat contient du pétrole, mais n'évitent pas un substrat huileux. La croissance ou la survie ne sont pas non plus affectées par des substrats contenant jusqu'à 1740 mg/litre de pétrole.

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DISPOSAL of oil into the sea has been the subject of many popular articles and recent scientific reviews (Nelson-Smith 1972; Butler et al. 1974; Anon. 1975). Some popular articles speculate about damage by oil pollution, but charges of "pollution" are often unjustified if no deleterious biological effects are predictable or demonstrated. Most damage from coastal oil spills has been of a localized and lethal nature (Anon. 1975). However, there is little knowledge of the concentrations of petroleum oils that may affect marine organisms upon long-term or continuous exposure (Mironov 1968; Tarzwell 1971; Blumer et al. 1973; Anon. 1975), especially organisms of the open ocean.

This study determines concentrations of oil in sea water that are toxic to a sensitive marine organism. Preliminary results were reported by Wells (1972). The study covers acute lethality and subacute and sublethal effects in exposures lasting up to 8 wk.

Venezuelan crude oil was chosen for testing because it is shipped to the Atlantic coast of Canada and accounted for 47% of crude oil imported in 1972 (Statistics Canada 1972). Larvae of the American lobster (*Homarus americanus*) were chosen as test organisms because planktonic crustacean larvae are often considered sensitive as a group; lobster biology and larval rearing techniques are fairly well known (Lewis 1970; Nowak 1972); eggs and newly hatched larvae are easily available over a protracted summer period; the species is an important member of inshore ecosystems (Mann and Breen 1972); and lobsters have considerable economic importance in Atlantic Canada and northeastern United States (Wilder 1970).

Methods

In brief, a stirred–ultrasonic dispersion of oil was diluted to obtain test concentrations. Newly hatched lobster larvae were exposed individually in glass jars containing 800+ ml of test water at 20 C. Larvae were fed brine shrimp (*Artemia salina*) daily, and test water was changed every 5 days. Observations were made on mortality, molting, and other parameters, during exposures of 4 and 30 days.

BIOLOGICAL ASPECTS

Egg-bearing female lobsters (*H. americanus*) were collected from the Gulf of St. Lawrence in summer and held over winter at St. Andrews, N.B., in running sea water at ambient temperatures. Groups of females were then held at different temperatures (1–17 C) so as to provide newly hatched larvae from April to October. General holding and acclimation procedures were those of McLeese and Wilder (1964). Just prior to hatching of eggs, each female was held separately at 15 C. Larvae were removed within 12 h of hatching, held at 18–20 C for 6–12 h, and fed large numbers of newly hatched brine shrimp (*A. salina*). Larvae were less than 24 h old at the start of tests.

Seven 4-day acute tests were done in 1971 with 242 larvae, individually contained in a 946-ml (32-oz) jar, filled to 15 cm by 800–810 ml of test water which was not renewed. Jars covered by petri dish lids were randomly assigned to positions in baths at 20 ± 1.0 C. Larvae were transferred by large-bore pipette and assigned by a completely randomized design. Each larva was fed 500–1000 brine shrimp nauplii in 5 ml of water, each day including the 1st day. Dead nauplii were not removed. A 14 L:10 D photoperiod was maintained using 40-W "Cool White" fluorescent lights, with light intensity at the test water surface being 270–540 lx. Dissolved oxygen was 3.9–5.8 mg/liter (average 4.8 mg/liter).

One 30-day test in 1971 and five in 1972, used a total of 450 larvae. Test water was replaced about every 5 days from a fresh dispersion by transferring each larva to a new container. Other conditions were the same as in 4-day tests, except that twice as many brine shrimp were supplied every 1 or 2 days. Dissolved oxygen was 3.5–6.8 mg/liter (average 5.5 mg/liter). Salinities were 25–31‰ (average 27.9‰) and pH was 7.5–8.4.

Some tests continued beyond 30 days, about the time that late fourth- or early fifth-stage postlarvae settle to the bottom. Polypropylene 4.5-liter containers were filled with 1 liter of substrate (coarse sand, gravel, and shells) at an even depth of 5 cm. From 0 to 870 mg of crude oil was spread over half the area of the substrate at middepth; there was no divider between oiled and unoiled sides. Unfiltered sea water (3.5 liters) was added to each container, at least one third being replaced daily. Temperature was 17–20 C. Postlarvae were fed with frozen shrimp and fish, and exuviae were returned after examination and invariably eaten.

Special tests were done in 1973 with 647 larvae. Food consumption of oil-exposed larvae was measured by adding known numbers of brine shrimp and counting those remaining or dead after 24 h. One 30-day test examined interrelations of different levels of feeding and oil concentrations. A group of 4-day tests compared effects of different dispersion methods and of filtering and aging dispersions, as described below.

Test containers were inspected at logarithmic intervals from 1 h to 4 days and daily thereafter. Moribund or dead larvae were examined microscopically in sea water; the criterion of death was lack of heartbeat. Larval stage was determined from characteristics given by Herrick (1911) and Templeman (1936a, 1948). Effective times to 50% mortality (ET50) were estimated by the methods of Litchfield (1949). Median lethal concentrations (LC50) and confidence limits were estimated by one of three standard pro-

grams of probit analysis (Finney 1971). Most 4-day LC50s were done by APL program 28 PROBIT (Institute of Computer Sciences, University of Guelph). Two to six cycles of iteration were used, until a plateau of maximum likelihood was reached. Thirty-day LC50s were done with the FORTRAN program BMDO3S (Dixon 1970). In some special experiments that lacked two partial mortalities between 0 and 100% the graphic-nomogram methods of Litchfield and Wilcoxon (1949) were used. Mortality in controls was always corrected according to Abbott's formula (Tattersfield and Morris 1924). Significant differences between LC50s were tested by SE of the difference (Litchfield and Wilcoxon 1949). Analysis of variance was conducted using the University of Miami FORTRAN program MANOVA.

Preparation of Test Water

Venezuelan Tia Juana medium crude oil was obtained from the Imperial Oil Ltd. refinery at Dartmouth, N.S. Its major properties were measured every 6 mo. Average characteristics of six measurements ± SE were: API gravity, ASTM D287 = 30.4 ± 0.1; specific gravity at 60 F = 0.8738 ± 0.0006, viscosity SUS at 100 F = 50.6 ± 0.3; acid number, ASTM D664 = 0.09 ± 0.01; sulphur % by weight = 0.96 ± 0.02; nickel and vanadium x-ray ppm = 15 ± 1 and 56 ± 1; and asphaltenes % by weight = 4.09. Oil was obtained in a 227-liter sealed drum in March 1971, sealed in 4.5-liter glass jugs, then stored in darkness at 18–20 C. At the beginning of each year's experiments, oil was sealed in completely full vials, and a fresh vial was used to make up each new dispersion.

Stock dispersions of oil in sea water were prepared by stirring and ultrasonic vibration. The intention was to simulate physical dispersion at sea, where oil-in-water dispersions form (Forrester 1971; Parker et al. 1971; Anon. 1973; Gordon et al. 1973). A stock dispersion was prepared by putting 4 liters of unfiltered sea water at 20–22 C in a 4-liter aspirator bottle and stirring magnetically at medium speed. An ultrasonic probe (1.3 cm titanium, frequency of 20 ± 0.4 kc/s, Artex Ultra-Sonic Dismembrator 300) was lowered 0.5 cm into the water and operated at 40% maximum intensity. Oil (400 mg) was introduced by syringe during 1–2 min, into the stirred and sonified water. The liquid was stirred and sonified for 30 min, settled for 15 min, and the dispersion removed through a bottom tap. From 4.4 to 14.8% of the dispersed oil was dissolved or in particles less than 1.2 μm, according to UV analyses after Millipore® filtration. Dilutions for test water were made up within 3 h as fixed fractions of the dispersion, brought to 20 C, and used in experiments about 17 h after initial dispersion.

Some special experiments used other methods: a) stirring without sonification; b) rapid and slow stirring for 24 h with maximum and minimum speeds of a magnetic stirrer; c) floating unstirred oil; d) filtration of standard dispersion through 1.2 μm Millipore® filters; and e) aging dispersions for 1 and 2 days before testing.

Measuring and Expressing Concentrations

Oil concentrations were measured by the UV method of Zitko and Carson (1970), modified mainly by dehydrating the organic solvent (n-hexane)-oil extract and by measuring concentrations at 253 nm. Accuracy and precision were satisfactory; a nominal 1.08 mg/liter in hexane showed an average 1.18 ± SE 0.00 mg/liter for four measurements and nominal 10.8 mg/liter showed 9.54 ± 0.53 mg/liter. Fluorescence spectroscopy as in Keizer and Gordon (1973) was used concurrently to measure many samples. Fluorescence measurements confirmed those by UV, the average UV to fluorescence ratio being 1.13 ± SE 0.22.

There was little loss of oil during dilution. Measured concentrations in various dilutions averaged 98% ± SE 13% of intended values. Routine measurements on all dilutions were therefore considered unnecessary. Concentrations throughout this paper are accordingly based on stock dispersions unless stated otherwise. Average initial measured concentrations (AIMC) are given for the 4- and 30-day tests. Concentrations are expressed as extractable organics, mg/liter. An average of all measurements on stock dispersions obtained during replicate experiments was used to characterize concentrations for that entire group of experiments. Tables give both nominal and measured concentrations. The nominal or theoretical concentration is calculated from the actual amount of oil initially added, without regard to whether it became dispersed or not.

In 4-day tests, the AIMC of nine stock dispersions prepared in 1971 was 18.0 ± 2.8 mg/liter (range 6–33 mg/liter), compared to the nominal value of 100 mg/liter. Stated values for particular test concentrations may not be completely accurate, as indicated by the SE and range. For the 30-day experiments in 1972, and in special experiments, an improved aspirator bottle changed measured concentrations significantly. The average of 15 dispersions used in 30-day tests was 7.4 ± SE 1.0 mg/liter (range 2.4–14.6 mg/liter). Thus for all 30-day tests, AIMC's are 7.4% of nominal concentrations. For the diverse group of special experiments, measured concentrations are treated individually, the basis in each case being obvious.

Initial concentrations have been used to characterize oil exposures, notwithstanding the decrease in oil concentrations between renewals (Fig. 1). After the first 2 days, measured concentrations in dilutions averaged 53 ± SE 6% of initial measured values, with a range of 30–87%. At the end of 4 days, concentrations averaged 34 ± SE 4% of initial values, with a range of 18–63%. Decreases were probably caused by oil floating to the surface, evaporation, chemical oxidation, and biodegradation. There was greater relative loss of oil fractions absorbing at 220 nm (Fig. 1). These measurements were made in the

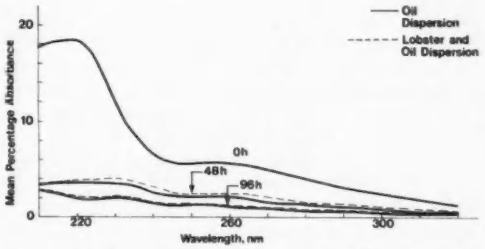

FIG. 1. UV absorption spectra for diluted ultrasonically stirred dispersions of Venezuelan crude oil, with and without single American lobster (*Homarus americanus*) larvae, over time.

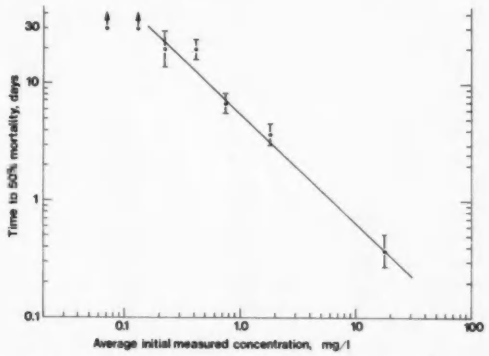

FIG. 2. Median mortality curve for lobster larvae, starting the test in their first stage and exposed to dilutions of dispersed Venezuelan crude oil. Curve fitted visually, using ET50s and 30-day LC50. ↑, indicates that an ET50 is greater than 30 days.

absence of lobster larvae, but representative spectra (Fig. 1) indicate that larvae had no major effect on measured oil fractions.

Results

The toxicity curve (Fig. 2) shows that mortality continued during 30 days. There is no obvious discontinuity between short- and long-term mortality, and hence no obvious threshold for acute lethality.

Four-day LC50s were 0.86 mg/liter for first-stage larvae and 4.9 mg/liter for third- and fourth-stage larvae (Table 1). The two values are significantly different. Results for the two later stages were similar but an accurate LC50 could not be estimated for fourth-stage alone because of low numbers of larvae. The 30-day LC50 was 0.14 mg/liter, lower by a factor of six than the 4-day LC50 for first-stage larvae, and significantly different. Overall control mortality was 21% in 4-day tests and 51% in 30-day tests.

Sublethal Effects

First- and third-stage larvae showed behavioral and color changes at lethal but not sublethal concentrations. At 18 mg/liter, lethal to all stages of larvae in 4 days, first-stage larvae quickly stopped swimming, contracted tightly, and changed from typical yellow–blue to red–yellow. They became moribund in 6 h and median time to death was 9 h. Fourth-stage larvae showed similar behavioral but no color changes at this lethal concentration. In 1.8 mg/liter, first-stage larvae suffered 64% mortality in 4 days, swam in a curled position, and changed color. Fourth-stage larvae lived and showed no behavioral or color changes at 1.8 mg/liter.

In 30-day tests, most deaths of first-stage larvae occurred during molting in the control, in concentrations below the 30-day LC50 (0.01–0.13 mg/liter), and in intermediate concentrations (0.24–0.41 mg/liter) (Fig. 3). Most often, death occurred at molting phase E_2, when the cephalothoracic carapace is thrown forward and the head and associated structures withdrawn (Aiken 1968). In the highest concentration (0.74 mg/liter) most deaths of first-stage larvae occurred before molting. Percentages of deaths during molting are significantly different among these three groupings of concentration (contingency table and chi-square, $P < .05$). For second- and third-stage larvae, most deaths were between molts, with no significant differences between groupings of concentrations. The reversed pattern of mortality, during molting from first-stage and between molts in stages 2 and 3, is significant within each concentration except the highest.

Dispersed oil affected rate of larval development. A comparison was made for 152 larvae which survived to fourth stage in 30-day tests. For the seven concentrations, 0, 0.01, 0.07, 0.13, 0.24, 0.41, and 0.74 mg/liter, average numbers of days taken to reach fourth stage were, respectively, 14.2, 13.8, 15.7, 13.3, 18.6, 17.3, and 17.1. Grouping above and below the 30-day LC50 shows significant differences among the control with average time of 14.2 days, the three lowest concentrations with weighted average time of 14.7 days, and the three highest concentrations with weighted average time of 17.9 days. Developmental time in high concentrations was significantly longer than in the other two groups. Developmental time in low concentrations was not different from the control (Duncan's multiple-range test). Developmental times within each stage showed the same differences, utilizing data from all larvae that successfully molted to

TABLE 1. Median lethal concentrations (LC50) in milligrams per liter, of dispersed Venezuelan crude oil for American lobster (*Homarus americanus*) larvae. AIMC = average initial measured concentration; N = Number of larvae; 95% confidence limits in parentheses.

Larvae		LC50, AIMC		LC50 nominal concn.	Probit line slope
Stage	N	4-day	30-day		
1	115	0.86 (0.40, 1.9)	—	4.8	2.01
3	98	4.6 (2.5, 8.6)	—	26	2.11
3 + 4	127	4.9 (3.0, 8.0)	—	27	2.32
1	450	—	0.14 (0.056, 0.23)	1.9	1.66

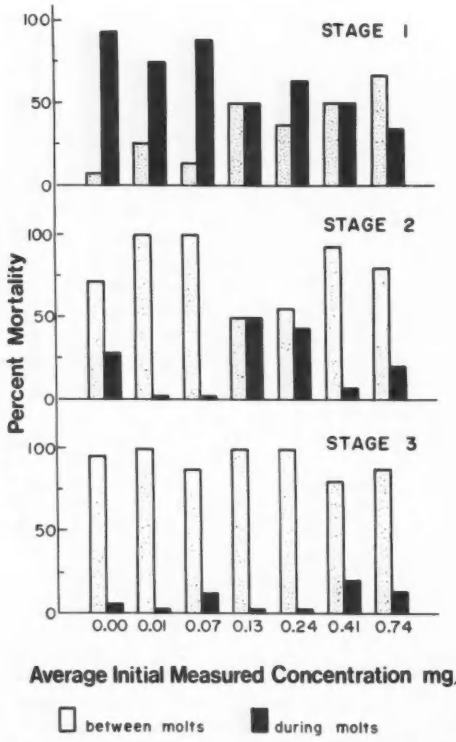

FIG. 3. Occurrence of mortality between molting and during molting for lobster larvae exposed from first stage to dilutions of dispersed Venezuelan crude oil.

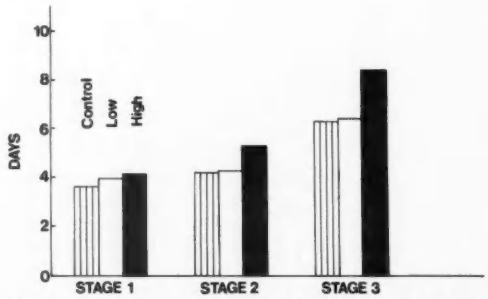

FIG. 4. Average developmental times of lobster larvae in 30-day exposures to dilutions of dispersed Venezuelan crude oil. Low concentrations are 0.01, 0.07, and 0.13 mg/liter, high concentrations are 0.24, 0.41 and 0.74 mg/liter. Only larvae that successfully molted to the following stage were included.

the next stage (Fig. 4; Scheffe's linear combination technique, Guenther 1965). Accordingly, the highest concentration having no effect on developmental time was 0.13 mg/liter.

"Intermediate" larvae (Templeman, 1936a) occurred more frequently in oil dilutions. Of 152 larvae reared to fourth stage in 30-day experiments, 11 retained characteristics of previous stages. All but two of these larvae remained planktonic instead of settling on the bottom. Five of the intermediates occurred in 0.24–0.74 mg/liter, five in 0.01–0.07 mg/liter, and one in controls. The occurrence of intermediates in oil concentrations (11.8% of larvae) is significantly different from controls (1.5% of larvae). The 11 intermediates spent an average of 17.9 ± 1.0 days in the first three stages, so their occurrence seems to be related to delayed development.

Food consumption was reduced in the presence of oil. In three trials involving 30 larvae, controls ate averages of 1.3, 1.7, and 1.9 times as many brine shrimp as did larvae in oil dilutions. The difference was significant by multivariate analysis of variance. Oil concentrations were 0.19 and 0.74 mg/liter AIMC. Food density, ranging from 450 to 1000 nauplii per day, also significantly changed average consumption. There was no

interaction of food density and presence of oil. Hence, during our regular experiments where all treatments were equally fed but both food and oil concentrations varied with time, effects are attributable to the presence of oil.

Oiled Substrate

Post-larval lobsters were not greatly affected by oil in the substrate. Following three 30-day experiments, 47 surviving fourth- and fifth-stage animals were reared over substrates. Seventeen survived to the eighth stage, but there was no significant difference in mortalities over clean substrate, and substrates containing three different amounts of oil. Nor was there any overall effect on rate of development or size of survivors. Only two differences were found. In fourth stage, larvae swam or walked in most containers, but in 1740 mg/liter of oiled substrate, the five lobsters sought shelter among pebbles or in burrows. The second difference was in number of burrows dug. Once settled, lobsters dug a single burrow when exposed to 0 mg/liter and 17–18 mg/liter but up to three burrows when exposed to 174 mg/liter and 1740 mg/liter. They made no significant choice between burrowing or occupying burrows on clean and oiled sides at any time during their exposures.

Other Methods of Dispersion

Crude oil dispersed by other methods was equally toxic as oil dispersed by the standard method, indicating that the latter was a representative way of putting oil into sea water.

One experiment compared toxicities of a standard dispersion and one made by stirring-only for 30 min. In standard dispersions, AIMC was 27.4% of nominal concentration, somewhat higher than most tests but within the normal range. In dispersions prepared by stirring-only, AIMC was only 0.65% of nominal concentration. The 10-day LC50 for 100 larvae in the standard dispersion was 0.41 (confidence limits 0.084, 2.0) mg/liter or a nominal concentration of 1.5 mg/liter. This is the expected value for 10 days (Fig. 2). In the stirred-only tests, concentrations were too low to cause appreciable corrected mortality. The highest concentration, 0.21 mg/liter AIMC and nominally 32 mg/liter, caused slightly less mortality than the control, again agreeing with the standard results. Four-day LC50s lead to the same conclusions. For both preparations toxicity was related to measured concentrations, with no indication that stirring-only selectively dispersed more-toxic fractions.

Dispersions stirred rapidly and slowly for 24 h were evaluated. Toxicity on the basis of measured concentrations again fitted results from the standard method of preparation. The 4-day LC50 for slow stirring was 0.40 (0.24, 0.65) mg/liter and for fast stirring was 0.80 (0.28, 2.3) mg/liter. Neither value is significantly different from the other, nor from the standard LC50. Much higher initial amounts of oil than in the standard procedure were required to obtain these measured concentrations. Only 0.20 and 0.26% of nominal concentrations were measured in the two stirred dispersions. Stirring is not particularly effective for dispersing oil into sea water, nor were long periods of stirring relatively more effective in dissolving the more-toxic fractions.

Another experiment tested the toxicity of crude oil, floating over 1.4 liters of water with a surface area of 104 cm^2. A nominal concentration of 317 mg/liter did not dissolve enough toxic components to cause any corrected mortality. There was only 0.55 mg/liter measured at 2 cm below the surface, somewhat less than the standard LC50. Oil components did not readily move downwards in the test water, concentrations at 10 cm depth equaling those in the control. There was no increase in measured oil at 2 cm depth from 48 to 96 h. Furthermore, amount of surface oil did not greatly influence the amounts that dissolved. Apparently only the layers of oil in contact with sea water were "active."

Filtrates

Bioassays with 166 larvae compared dilutions of standard dispersions with dilutions of the same parent dispersions after filtration through 1.2 μm Millipore® filters. As measured in dilutions, the filtrates had an average concentration only 12 ± 3.8% of that in the unfiltered dispersions. The 4-day LC50s of the filtrates and unfiltered dispersions were 0.61 (.42, .89) mg/liter and 1.5 (1.1, 2.0) mg/liter, respectively. Hence, constituents of filtrates were more toxic per unit measure than the combined constituents of whole oil dispersions.

Aging

Toxicity of diluted dispersions aged 0, 24, and 48 h was examined in four trials with a total of 110 larvae. Four dispersions prepared for the trials had initial measured concentrations of 2.80, 4.43, 4.48, and 26.0 mg/liter.

Dilutions (0.32) of the dispersions lost oil fractions upon standing, toxicity decreasing in proportion to loss. After standing for 1, 2, 3, and

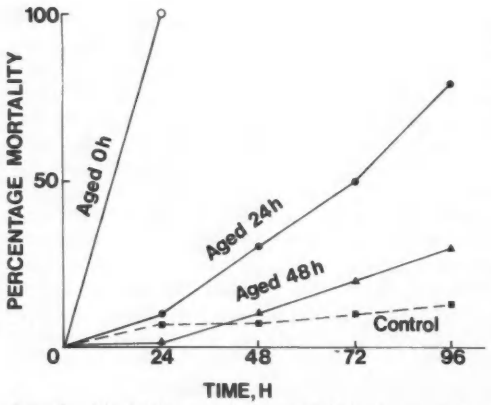

FIG. 5. Mortality over 4 days of lobster larvae when exposed to dilutions of dispersed Venezuelan crude oil aged for 0, 24, and 48 h. The decrease in toxicity was related to lower amounts of oil as measured chemically. These results are pooled values for two dispersions of similar concentrations.

4 days, average measured oil concentrations were 71, 41, 34, and 30%, respectively, of initial concentrations, very similar to the loss described in Methods. Toxicity of dilutions decreased with aging, as indicated by combined results for two dispersions having almost identical concentrations (Fig. 5). Mortality after 24-h to 72-h exposure was significantly lower for the 1-day-old dilution than for fresh dilutions (contingency table and chi-square). The 2-day-old dilutions caused significantly less mortality than the day-old dilution, after 72- and 96-h exposure, and did not cause significantly more mortality than seawater controls.

This loss in toxicity was proportional to loss in measured concentration with aging, although results are somewhat fragmentary. The 4-day LC50 for fresh dispersions was 1.1 mg/liter, almost the same as the standard LC50 of 0.86 mg/liter. For 1-day-old dispersions, an AIMC of 0.76 mg/liter caused a corrected mortality of 61%, reasonably fitting the standard results for fresh dispersions. For 2-day-old dispersions, three AIMC's gave an LC50 of 1.8 mg/liter, not significantly different from the standard LC50 of 0.86 mg/liter for fresh dispersions, nor from the 1.1 mg/liter obtained for fresh dispersions. This signifies that the chemical measurements adequately measured toxic components, i.e. there was no indication of a proportionately higher loss of more toxic fractions during aging of oil dispersions.

REFERENCE TOXICANT

Dodecyl sodium sulphate (DSS), tested with first-stage larvae and the same procedures used for oil, had a 2-day LC50 of 3.5 mg/liter (1.8, 6.7, 2.28) and 4-day LC50 of 0.72 mg/liter (0.44, 1.2, 4.12), bracketed figures being confidence limits and slope, respectively.

Discussion

Acute toxicity of Venezuelan crude oil was consistent with measured concentrations. Four-day LC50s based on measured oil were the same for oil dispersed into water by several methods: stirred–sonified; stirred-only for long and short periods and at different speeds; dispersed and aged for 2 days. In this study, spectra showed that fluorescing constituents of dispersed oil that entered the water were similar in these cases. Recent open tank experiments with spilled crude oils showed that oil constituents are accommodated by physical mixing and solubilization into sea water in a similar manner (Wells and Keizer 1975; Gordon et al. 1976). The corollary to the above findings is that measurement of dispersed oil by spectroscopy, UV or fluorescence, is a satisfactory way of assessing toxicity of this crude oil in sea water.

However, one experiment showed that composition as well as measured concentration determined acute lethality. When sonified–stirred dispersions were filtered, oil constituents that passed the filter were more toxic per unit measure than constituents of the unfiltered dispersions. If one can assume additivity of toxic contributions of soluble (dissolved and subparticulate) constituents and particulate (filterable) constituents of the standard dispersion, the following relationship exists:

$$\frac{\text{Concn of dispersion}}{\text{LC50 of dispersion}} = \frac{\text{Concn of solubles}}{\text{LC50 of solubles}} + \frac{\text{Concn of particulates}}{\text{LC50 of particulates}}$$

$$\frac{1}{1.5} = \frac{0.12}{0.61} + \frac{0.88}{\text{LC50 of particulates}}$$

Hence, the LC50 of particulates is 1.8 mg/liter, one-third the toxicity of soluble constituents, significantly lower if it is assumed that confidence limits on the former are proportional to those on the latter. Dissolved and subparticulate oil would probably more easily enter aquatic animals and poison them. Highly soluble fractions such as low-boiling saturated hydrocarbons and low-boiling aromatics, especially benzenes and naphthalenes, are among the more toxic constituents of oil (Blumer 1971; Boylan and Tripp 1971; Moore and Dwyer 1974, among others).

The nominal or "added" concentrations of oil

are of little value in toxicity experiments, in view of the differences obtained with different methods of dispersion. Comparisons between results of different investigators, based on nominal concentrations, could be quite inaccurate unless exactly the same dispersing procedures were used.

Hence, the 4-day lethal concentrations of 0.86 mg/liter of oil for first-stage larval lobsters, and 4.9 mg/liter for third and fourth stages, will be compared only with toxicity results in the literature which are based on concentrations measured by spectroscopy. Rock crab larvae (*Cancer productus*) had a 96-h LC50 of 3.2 mg/liter of No. 2 fuel oil (Vaughan 1973), about the same as our third- and fourth-stage value, although the oils are different. Rock crab larvae were surprisingly resistant to dispersed Louisiana and Kuwait crude oils, with 4-day LC50s of 220 mg/liter and 250 mg/liter, respectively (Vaughan 1973). Post-larval stages of *Penaeus* had a 96-h LC50 greater than 20 ppm water-soluble fraction of Louisiana crude oil (Anderson et al. 1974). Two-day LC50s of Louisiana and Kuwait crude oil were 8.7 and 6.6 ppm for adult mysids, *Mysidopsis almyra*, and greater than 17 and 10 ppm for adult grass shrimp, *Palaemonetes pugio* (loc. cit.). Calculations from data of Percy and Mullin (1975) indicate 4-day LC50s for Venezuelan crude oil, with concentrations measured after the 1st day of exposure, of 29 mg/liter for adult amphipods, *Onisimus affinis*, and greater than 82 mg/liter for adult copepods, *Calanus hyperboreas*.

Our results are at the low end of this range, indicating that lobster larvae are relatively sensitive to oil. Indeed, the value for first-stage larvae seems to be the lowest published value for acute toxicity of crude oil to an aquatic animal. Our LC50 of 0.72 mg/liter for the reference toxicant DSS is lower than LC50s of 2 mg/liter for an adult marine mysid and 14 and 108 mg/liter for grass shrimp (Anderson et al. 1974; McAuliffe et al. 1975) and so lobster larvae seem to be generally sensitive animals.

Some other toxicants have been tested against lobster larvae. Pulpmill waste had an acute lethal threshold of about 100,000 ppm (Sprague and McLeese 1968). A nonionic oil dispersant had an LC50 of 46 mg/liter (Engel and Neat 1971). The 48-h LC50 of copper for larvae of *Homarus gammarus* was about 0.2 mg/liter and of mercury was about 0.07 mg/liter (Connor 1972), slightly below the 4-day LC50 for oil for first-stage larvae. Insecticides are very toxic to crustaceans, and the 4-day LC50 of the organophosphate fenitrothion was 0.001 mg/liter for lobster larvae (McLeese 1974). Our acute results of 0.86 to 4.9 mg/liter are near the middle of this range. Venezuelan crude oil must therefore be considered a reasonably toxic material.

The 30-day LC50 of 0.14 mg/liter for crude oil is low, about the same as the acute toxicity of copper. No other values in the literature were found for similarly long exposures, but 4 ppm of Venezuelan light crude lowered the survival rate of larval crabs, *Neopanope texana*, over 14 days (Katz 1973).

The "safe" level of crude oil, which did not cause observable sublethal effects, approximates the 30-day LC50. The highest level that did not retard development through the first four stages was 0.13 mg/liter. Concentrations of 0.24 mg/liter and above caused retardation and the logarithmic average of these two numbers is 0.18 mg/liter, close to the 30-day LC50. Such delayed development is probably a sensitive indicator of sublethal effect and was also observed with crab larvae and crude oil (Katz 1973), and insecticides in various studies summarized by Wells (1976). In nature, delayed development would keep lobster larvae planktonic for longer times, increasing their exposure to predators and surface drift.

In addition, first-stage larvae showed different proportions of deaths at molting and between molts, for concentrations of 0.13 mg/liter and below, compared to concentrations of 0.24 mg/liter and above. Crude oil has also been shown to decrease molting success in Tanner crabs *Chionoecetes bairdi* (Karinen and Rice 1974). Stewart and Squires (1968) consider that "any stress situation would be expected to delay or inhibit ecdysis" in lobsters.

Food consumption was decreased at 0.19 mg/liter, slightly above the 30-day LC50, but it was not documented whether this occurred at lower concentrations. Lower food consumption may have resulted from weakening of larvae in oil, interference with chemoreception and food detection, or change in palatability of oiled *Artemia* nauplii. Small amounts of crude oil interfered with chemoreception and feeding behavior of adult lobsters (Atema and Stein 1974). The amphipod *Onismus* chooses clean food over tainted food and generally avoids tainted food presented alone, although an isopod *Mesidotea* shows no such discrimination (Percy and Mullin 1975). Decreased food consumption of lobster larvae in oil may have been a contributing factor in both slower development and increased frequency of "intermediate" larvae (Templeman 1936a, b; Kurata 1959, 1962; Corey 1963 unpublished data).

It may be reasonable that sublethal effects were not detected below the 30-day LC50. Thirty days represents an exposure time about equal to the

entire larval life at 20 C, and any deficiencies in functioning could lead to death in delicate larval stages.

The ratio of 30-day LC50 (first to fourth-stage larvae) to 4-day LC50 of third and fourth stages is 0.029. The ratio is 0.16 for the 4-day LC50 of first-stage larvae. The first ratio is more meaningful since the 30-day value depends mainly on resistance of later-stage larvae. This ratio of about 0.03 is in the middle of the usual range of 0.1–0.01, found for such safe to lethal ratios in toxicity work with fish (Sprague 1971). Percy and Mullin (1975) found that the activity of an amphipod was impaired at about 0.3 of the acute LC50, but no sublethal impairment was evident for an isopod. A ratio of 0.08 was obtained for the highest concentration of used crankcase oil that did not affect reproduction of the flagfish *Jordanella* (Hedtke et al. 1974).

The harmful concentrations stated for lobster larvae are conservatively high since they are based on initial concentrations. Average concentrations might be a better way of representing exposures, since 2-day-old dispersions retained toxicity based on measured concentrations. Average concentrations during exposures would be 59% of initial concentrations, according to the usual arithmetic averaging procedure.

There was considerable mortality among controls. Such mortality is expected when lobster larvae are reared, even singly, in the laboratory. Our results are similar to those of Sprague and McLeese (1968) who found 50% mortality in 14 days, among lobster larvae in control tests. Our correction for control mortality by Abbott's formula is the standard one in probit analysis and is the only rational one available. It did not compensate for any interaction that may have occurred between mortality caused by oil and by other factors in laboratory rearing.

The lack of major effects of oily substrate on post-larval lobsters is somewhat surprising. Such effects may occur in nature, but even at fairly substantial levels of substrate contamination, only increased burrowing activity was documented.

Present background levels of petroleum hydrocarbons in the ocean are one or more orders of magnitude lower than the 30-day LC50. Surface waters off eastern Canada have concentrations from 0.002 to 0.02 mg/liter (Gordon and Keizer 1974; Gordon et al. 1974b). In harbors and areas of tanker traffic there are concentrations from 0.002 to 0.07 mg/liter (Michalik and Gordon 1971; Gordon et al. 1974a). However, oil spills could damage local populations of larvae from midsummer to midautumn. Concentrations under experimental spills were only as high as 0.05 mg/liter (Wells and Keizer 1975), but under real spills in eastern Canada, they were up to 0.8 mg/liter (Gordon et al. 1973) which is about equal to the 4-day LC50.

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Utilization of Artificial Shelters by the American Lobster (*Homarus americanus*)[1]

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SHEEHY, D. J. 1976. Utilization of artificial shelters by the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 33: 1615–1622.

Artificial shelters, fabricated of pumice concrete and placed in areas devoid of natural shelter, were readily colonized by American lobsters (*Homarus americanus*). Two designs, single chamber and triple chamber, were used for the shelters. Although they both afforded approximately the same available volume, it was demonstrated that those of triple chamber design were utilized by a larger number of lobsters per shelter. Spacing and orientation also had a significant effect on occupancy. Lobster abundance and biomass observed on shelter sites were equal to or greater than those reported for good natural grounds. The shelters were used by both juvenile and adult lobsters.

SHEEHY, D. J. 1976. Utilization of artificial shelters by the American lobster (*Homarus americanus*). J. Fish. Res. Board Can. 33: 1615–1622.

Des abris artificiels, fabriqués de ciment pierre ponce et placés dans des régions dépourvues d'abris naturels, sont rapidement colonisés par des homards américaines (*Homarus americanus*). Nous avons utilisé deux types d'abris, à une chambre et à trois chambres. Bien que les deux types aient fourni à peu près le même volume, le type à trois chambres a été utilisé par une plus grand nombre de homards par abri. L'espacement et l'orientation ont également un effet significatif sur l'occupation. L'abondance et la biomasse des homards observés sur les aires d'abris artificiels sont égales ou supérieures à celles signalées sur de bons bancs naturels. Les abris sont utilisés tout autant par les jeunes que par les adultes.

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EFFORTS to increase American lobster (*Homarus americanus*) populations have been stimulated by intense consumer demand and the resultant fishing pressure. Lack of natural shelter may be a limiting factor in the distribution of lobsters in inshore areas (Stewart 1970; Cobb 1971). Artificial additions to the seafloor have been successful in attracting and providing shelter for many marine organisms (Carlisle et al. 1964; Unger 1966; Scarratt 1968, 1973; Stone et al. 1973).

In the most extensive of these studies, Scarratt (1968, 1973) conducted an investigation to determine whether or not the scarcity of suitable cover was a limiting factor to inshore lobster populations. The study involved the construction of a quarried rock reef covering over 2700 m² in 17 m of water in Northumberland Strait in eastern Canada. Although lobster biomass after 7 yr was greater than or equal to that on nearby productive grounds, Scarratt (1973) concluded that cheaper sources of material and placement methods would be required for economic reef construction.

The objective of the present study was to assess the use of diver-deployed unit artificial shelters that had been designed for lobster occupancy. The effects of spacing, orientation, and compartmentalization were evaluated and the nature of seasonal trends was examined.

Materials and Methods

DESIGN AND FABRICATION

Both single and triple chamber shelter units, fabricated commercially from pumice concrete, were used (Fig. 1A, B). Pumice concrete was chosen for its endurance and inertness in sea water as well as for the flexibility of shape that it permitted. It had a density of 1.36 g/cm³ and a rough texture. Units were formed by injecting the mix into a die under pressure in a manner similar to that used in the fabrication of common cinder blocks.

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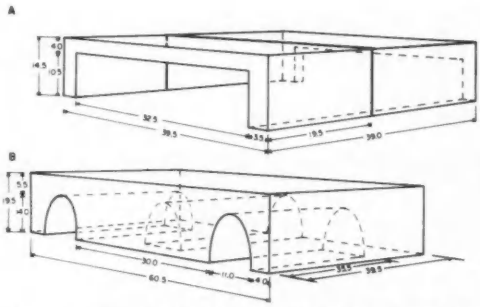

FIG. 1. Artificial shelters fabricated from pumice concrete. A, Single chamber unit; B, triple chamber unit. Dimensions in centimeters.

The dry weight of a complete single unit was 9.1 kg and of a triple chamber unit, 36.3 kg. Due to size restrictions in fabrication, both shelters were constructed in sections. These were placed together in the case of the single unit shelter and glued together with scarabond mortar in the case of the triple chamber unit. The low profile shape of the single chamber shelter was based on Cobb's (1971) observations of natural burrow dimensions. The triple chamber unit was designed (within manufacturing limitations) to provide a comparison for the single chamber unit. The total volume of shelter provided by both types of shelters was similar, being 0.013 m^3 for the single and 0.014 m^3 for the triple chamber unit. This represented a difference of less than 10%, close enough to afford a reasonable comparison between units offering similar shelter volume.

SITE SELECTION AND DEVELOPMENT

Preliminary study — A preliminary study to evaluate the overall feasibility of unit artificial shelters was initiated using single chamber shelters. It was designed to assess the effects of intershelter distance and shelter orientation (with respect to wave action and current direction) on occupancy by lobsters and shelter stability on the bottom.

The site was located inside the east gap of the Point Judith Harbor of Refuge, Point Judith, Rhode Island (Fig. 2, site A); mean water depth was 6.4 m. Substrate was a sandy sediment with a mean particle diameter of 0.14 mm. This area was selected for ease of access, flat sandy bottom devoid of resident lobsters, proximity to nearby populations, and the fact that predominant wave and current directions are generally perpendicular to each other. The nearest area supporting resident lobsters was the breakwater wall of the Harbor of Refuge, which was about 600 m distant.

The basic design in which the units were placed was a square matrix containing 7 rows and 7 columns of shelters, each at a prescribed distance from the next. An L-shaped array of 8 of these matrices (392 shelter units) was constructed by divers during late September and early October 1972. Shelters were lowered to the bottom on pallets and placed in the array of sites where divers had previously placed marker buoys. Each arm of the L-shaped array had 4 matrices, with shelters spaced at 30-, 61-, 122-, 244-cm (1, 2, 4, 8 ft), intervals (Fig. 3). The axis of one arm of the array was parallel to the predominant direction of bottom current (and roughly perpendicular to predominant wave direction), with shelters oriented with their open ends into the current. The axis of the other array arm was perpendicular to the general current direction (parallel to wave direction) and contained shelters oriented with their closed ends into the current.

Comparison study — The site selected for the comparison study of lobster occupancy in single and triple chamber units was located in the entrance channel to Salt Pond, inside the Point Judith breakwater in about 5.6 m of water (Fig. 2, site B). This area is characterized by strong tidal currents ranging up to 125 cm/s (2.5 knots) and no significant wave action.

The sediment in the channel was coarse sand (mean particle diam 0.30 mm) with extensive shell fragments that provided a stable base for the heavier triple chamber shelters. There were some resident lobsters in this area, but in general their burrows were confined to the channel banks, where rooted vegetation and finer sediment permitted burrowing. Extensive man-made debris also provided additional shelter.

The single and triple chamber units were installed by divers on November 3 and 25, 1972, respectively. One 7 × 7 matrix of each type was deployed in the same manner as in the preliminary study with 244-cm (8 ft) intershelter distance.

MONITORING

Divers recorded the number and estimated size of

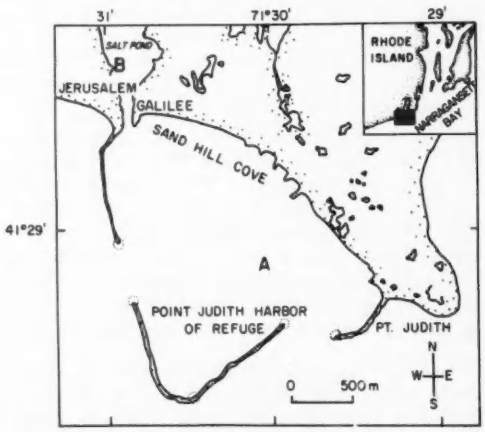

FIG. 2. Point Judith, Rhode Island, showing location of shelter study sites (A and B). Insert: Narragansett Bay, Rhode Island.

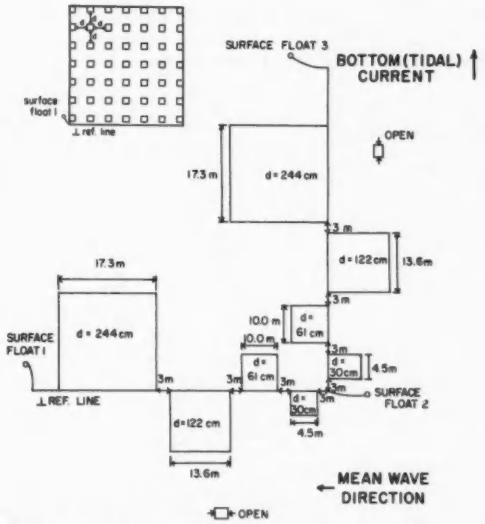

FIG. 3. Deployment of single chamber shelter matrices in the Harbor of Refuge with reference to mean current and wave directions. Insert: expanded view of individual matrix.

lobsters as well as the number and species of other crustaceans and fish for each shelter that was examined during each survey. A relative size scale was used to assess changes of differences in the size composition of lobsters. This was done visually because it was felt that handling might influence occupancy and would also be time consuming. Lobsters estimated to be less than 7.5-cm TL were classified as small, 7.5–15.0 cm — medium, and longer than 15.0 cm — large (TL — tip of rostrum to posterior margin of telson). A test survey in which actual measurements were made after size-class assignment by divers indicated that lobsters were assigned to the correct category with 85% accuracy.

The single chamber shelters of the preliminary study (site A, Fig. 1) were monitored on November 1 and 22, 1972, December 13, 1972, January 15, 1973, and September 13, 1973. The November 1972 surveys were complete, with the exception that only 22 of the 49 units in the 30-cm matrix were monitored on November 1, 1972 due to time limitations. Partial surveys of 6 shelters from each of the 4 matrices (24 shelters/survey) were conducted on December 13, 1972, January 15, 1973 and September 13, 1973. The shelters surveyed were selected by using a table of random numbers.

In the comparison study, single chamber shelters were monitored at least once a month from November 1972 to February 1974, with the exception of February 1973 and January 1974 (Table 4). More frequent observations were made immediately after installation to determine the rapidity with which the units were occupied. Triple chamber shelters were monitored monthly from December 1972 until January 1974 with the exception of February 1973. Complete surveys of all available shelters were accomplished on each survey date until February 1974; partial surveys were conducted of each site on March 1, and July 20, 1974.

A final sample survey of each matrix was conducted in January 1975 to obtain a biomass estimate of the lobster populations occupying the shelters. Divers, using a table of random numbers, selected shelters from each matrix and collected all lobsters that were observed until a sample of at least 40 lobsters was obtained from both the single and triple chamber shelters. Carapace lengths were then taken and biomass estimates made using Cobb's regression equation for Rhode Island lobsters: log wt = 3.0885 log(carapace length) − 3.2662, where weight is expressed in grams and length in millimeters.

Results

Evaluation of Preliminary Study (Site A)

During the interval between installation and the first systematic survey on November 1, 1972, two major storms occurred. About 80% of the 196 shelters with open ends perpendicular to the current (current flowing through the shelter) were flipped over by wave action and were in disarray.

In contrast, those shelters with open ends parallel to the current (current striking the closed end of the shelter) were stable and relatively undisturbed. Slight separation of the two sections making up a shelter unit were observed; however, in most cases the desired stable position was retained. In this case, the bottom currents striking the closed end of the shelters had scoured the sediment away from the legs, allowing them to sink into the sediment for anchorage. As the legs sank deeper into the sediment, the surface area presented to the current became smaller and therefore a reduction in scouring occurred. The majority of the shelters had stabilized when the roof was between 4 and 8 cm above the substrate. This permitted lobsters to burrow easily into the shelter. Because I was primarily interested in the results of a stable shelter unit, data collection was subsequently confined to those 196 shelters with the closed ends oriented into the current.

The influence of intershelter distance proved to be important from a physical perspective. During the surveys conducted on November 1 and 22, 1972, it was observed that in the 30- and 61-cm (1 and 2 ft) interval matrices, the level of the substrate within the matrix was 5–13 cm lower than outside the matrix. Apparently the combined effect of wave and current action was acting on the substrate within these matrix blocks as a single unit, effectively sinking the whole

TABLE 1. American lobster (*Homarus americanus*) occupancy of single chamber shelters in Harbor of Refuge (site A).

	Spacing interval (*cm*)	No. examined	No. occupied	Total lobsters	Size[a]		
					L	M	S
Nov. 1, 1972	30	22	12	12	3	7	2
	61	49	36	36	1	17	18
	122	47	30	30	3	12	15
	244	49	47	55	16	18	21
Nov. 22, 1972	30	49	35	47	6	18	23
	61	49	46	54	3	30	21
	122	49	32	35	3	17	15
	244	49	46	55	13	19	23
Dec. 13, 1972	30	6	5	5	1	3	1
	61	6	6	8	2	4	2
	122	6	6	6	0	4	2
	244	6	6	9	2	4	3
Jan. 15, 1973	30	6	5	5	0	2	3
	61	6	6	6	2	3	1
	122	6	5	5	1	2	2
	244	6	6	7	2	3	2
Sept. 13, 1973	30	6	6	8	2	4	2
	61	6	6	7	2	3	2
	122	6	6	10	2	4	4
	244	6	6	9	3	3	3

[a]See text for details; L = large, M = medium, S = Small.

matrix below the normal substrate levels. Therefore, they were nonfunctional.

A summary of the results of the surveys that were conducted on November 1 and 22, 1972, December 13, 1972, January 5, 1973, and September 13, 1973 is presented in Table 1. The total number of lobsters observed in the single chamber shelters in the Harbor of Refuge on November 1, 1972 was 133 (169 shelters examined), and on November 22, 1972 was 191 (195 shelters examined). The random samples on December 13, 1972, January 15, 1973 and September 13, 1973 indicated that lobsters continued to occupy the shelters during the winter and that shelters were still being used by lobsters 1 yr after installation. Thomas (1968) gave evidence of lobsters overwintering in natural burrows. Among lobsters observed in the September 1973 survey were egg-bearing females and newly settled post larvae.

The percentage of shelters occupied by more than one lobster was 10% on November 1, 1972, increased to 17% on November 22, 1972, and was 35% for sample data collected on September 25, 1973. Multiple occupancy was not significantly affected by intershelter distance to any demonstrable degree.

An analysis of variance was performed on the data from the surveys conducted on November 1 and 22, 1972. A four-way full factorial design was used. Spacing (61-, 122-, and 244-cm intervals), survey days (November 1 and 22), lobster size (small, medium, and large), and shelter location (perimeter or internal) were the four main effects tested. Each matrix was partitioned into a perimeter and an internal section to determine if lobster distribution was influenced by shelter location within the matrix itself. Data from the 30-cm internal matrix was omitted from the analysis because the November 1, 1972 survey of this matrix was incomplete.

The results of the analysis indicated that the variance attributable to survey date, spacing interval, and lobster size is significant ($\alpha = 0.01$). While area (perimeter vs. internal) is not significant by itself, the F values obtained in testing the interaction of area–lobster size as well as spacing interval–lobster size are highly significant ($P < 0.01$), implying that the lobster size distribution is highly related to both the shelter spacing interval and to whether the shelter is located on the perimeter or internal section of a matrix. An examination of the cell means indicates that small- and medium-size lobsters are responsible for these significant interactions. The distribution of large lobsters (> 15.0 cm TL) within the

TABLE 2. Single unit shelter data, shelters installed November 3, 1972 in Salt Pond Entrance Channel.

Date	Temp (C)	Available shelters	Total lobsters	Size			No. multiple occupancy
				L	M	S	
Nov. 7, 1972	10.0	49	19	0	8	11	0
Nov. 11, 1972	11.1	49	30	0	3	28	1
Nov. 17, 1972	8.0	46	28	1	7	20	0
Dec. 9, 1972	6.8	44	49	3	19	29	4
Dec. 14, 1972	6.4	49	38	10	26	2	1
Dec. 27, 1972	5.0	48	54	11	35	8	8
Jan. 17, 1973	2.5	46	43	5	26	12	5
Mar. 15, 1973	5.5	43	38	14	19	7	4
Apr. 14, 1973	6.1	46	56	7	34	13	9
May 10, 1973	11.0	48	56	13	29	14	10
June 13, 1973	16.5	42	49	14	22	13	11
July 19, 1973	19.1	39	47	12	26	9	12
Aug. 23, 1973	20.2	35	55	10	33	12	17
Sept. 27, 1973	16.9	37	56	17	25	15	16
Oct. 23, 1973	13.5	38	45	14	27	4	5
Nov. 21, 1973	8.5	36	51	12	25	14	13
Dec. 29, 1973	6.0	36	57	11	33	13	19
Feb. 1, 1974	2.1	36	41	8	25	8	6
Mar. 1, 1974[a]	3.0	12	18	1	10	7	7
July 20, 1974[a]	17.6	33	51	15	25	9	16

[a]Sample survey.

matrix was inconsistent, but the number of large lobsters within the 244-cm (8 ft) interval matrix was more than twice that of any other matrix observed during both November surveys.

While the results of this analysis strongly suggest the significance of the above-mentioned interactions, no definitive conclusions can be drawn since the analysis was performed on a relatively small sample. Furthermore the normal distribution of the sample was questionable. Work currently in progress in this area will produce a greater amount of data that can be evaluated by multiway contingency table analysis, which does not require any assumptions about the normality of the population.

EVALUATION OF COMPARISON STUDY (SITE B)

The data on lobster occupancy for single and triple chamber units are presented in Tables 2 and 3, respectively. Multiple occupancy refers to the shelters that are occupied by more than one lobster. The mean number of lobsters per shelter and the percent multiple occupancy for each shelter type are plotted in Fig. 4.

A multivariate analysis of variance and covariance was conducted on the data obtained from the study that compared single and triple chamber shelters. The analysis was conducted by assuming a one-way classification with two levels. Type of shelter was the treatment, and single and triple chamber units were the two levels of treatment. This treatment was tested by measuring the two variables: number of lobsters and number of incidences of multiple occupancy.

Since the number of available shelters of each type varied during the course of the experiment, the variable (number of available shelters) was included in the analysis as a covariate because the number of lobsters and number of multiple occupancies were assumed to be dependent on the number of available shelters. Results of the analysis of variance due to the group effect (type of shelter) measured on the two variables demonstrated that the type of shelter is highly significant ($P < 0.01$) on both number of lobsters and incidences of multiple occupancy.

Results indicated up to 60% occupancy of both shelter types within a week. Allowing a month for initial occupancy, the mean number of lobsters per shelter for the next 12 mo averaged 1.25 for single and 2.12 for triple chamber units. Some fluctuations in occupancy of the shelters by lobsters were also indicated. The major species other than lobsters that also used the shelters included Cancer crabs (*Cancer irroratus*, *C. borealis*), cunner (*Tautogolabrus adspersus*), toadfish (*Opsanus tau*), and sculpins (*Myoxocephalus*).

TABLE 3. Triple chamber shelter data, shelters installed November 25, in Salt Pond Entrance Channel.

Date	Temp (C)	Available shelters	Total lobsters	Size			No. multiple occupancy
				L	M	S	
Dec. 10, 1972	6.8	42	64	21	27	16	22
Dec. 15, 1972	4.2	49	63	10	47	6	17
Dec. 29, 1972	4.0	49	91	22	67	6	36
Jan. 16, 1973	2.0	49	114	23	85	6	46
Mar. 15, 1973	5.5	49	84	16	68	16	32
Apr. 9, 1973	6.1	49	99	13	64	22	37
Apr. 23, 1973	10.0	49	102	12	59	31	40
May 10, 1973	11.1	49	99	8	60	30	42
June 12, 1973	17.0	49	106	15	54	37	42
July 20, 1973	18.2	48	121	25	62	34	46
Aug. 22, 1973	21.1	48	124	32	62	30	43
Sept. 27, 1973	16.9	47	110	34	38	38	42
Oct. 21, 1973	13.5	47	84	35	38	11	28
Nov. 22, 1973	8.5	49	105	29	51	25	39
Jan. 12, 1974	4.1	41	116	33	62	21	41
Mar. 1, 1974	3.0	18	46	21	17	8	17
July 20, 1974	17.6	14	35	10	18	5	13

[a]Sample survey.

The decline in lobster occupancy noted in late October occurred just prior to a mass molt during the November survey when many lobsters were in the paper or leather shell condition. This observation is similar to that noted by Stewart (1970). During the November decline in lobster numbers, occupancy by the toadfish increased 50% over the October survey levels.

A luxuriant growth of fouling organisms developed on the shelters during the course of this study. The major species involved were *Mytilus edulis*, *Asterias vulgaris*, *Lammaris*, *Chondrus*, and *Fucus*, as well as several bryozoans and hydroids. Weiss (1970) indicated that mussels and starfish as well as plant material contribute to the diet of the lobster. Many species of fish were observed to use the shelter and attached organisms for cover. By the end of the survey, the shelters could barely be recognized as artificial additions.

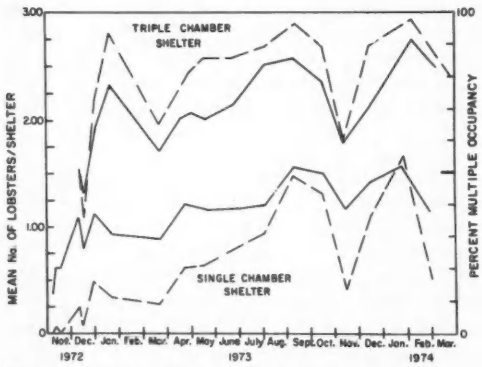

FIG. 4. Shelter occupancy by American lobsters (*Homarus americanus*). Mean number of lobsters per shelter(———) and percent multiple occupancy (– – –) for single and triple chamber units.

Maximum multiple occupancy occurred in late December and early January, with a second peak in July and August. These maxima occurred just after periods during which a high incidence of postmolt lobsters were observed (mid-September–early December and mid-April–mid-June). Multiple occupancy exceeded 50% in only one survey of single chamber units. For the triple chamber units, multiple occupancy consistently exceeded 65%, with the exception of the two initial observation periods, and reached a maximum of 96%.

A final survey was conducted on January 3 and 4, 1975 during which a sample of at least 40 lobsters was collected from each matrix. The results of this survey (Table 4) indicated that the triple chamber units had a greater biomass per unit area (74.2 as opposed to 43.1 g/m^2) than the single chamber units. There was no significant ($P > 0.05$) size difference in lobster samples from the two matrices.

Discussion

The results indicate that lobsters will readily occupy artificial shelters of both single and triple

TABLE 4. Lobster biomass estimates for single and triple chamber units after 25 mo.

	Single chamber	Triple chamber
No. shelters sampled	22	14
No. lobsters collected	40	41
Mean carapace length (*mm*)	56.2	59.6
SD	20.5	20.0
Range (CL) (*mm*)	10.5–88.0	19.7–92.0
Estimated total lobsters collected[a]	7592.1	8953.2
Area surveyed (m^2)[b]	176.3	120.7
Biomass estimate (g/m^2)	43.1	74.2
% legal	12.5	17.1

[a]Calculated using Cobb's (1969) regression equation for Rhode Island lobsters.

[b]Area computed as ratio of total area based on the number of shelters sampled.

chamber configurations. Lobster abundance per unit area observed during this study appears to be a function of both shelter spacing and number of compartments per shelter. While it would be most desirable to compare lobster abundance on the basis of biomass per unit area, information was not initially available due to the lack of sensitivity of the size classification. Lobster abundance does appear to be greater than that recorded by other investigators for natural habitat (Cobb 1971; Stewart 1970) and either equal to or greater than that observed by Scarratt (1973) on an artificial reef.

Cobb (1971) surveyed three circular plots of 530 m^2, one each on bottom characterized by rock, mud, and sand. The rocky area yielded an average of one lobster every 10.2 m^2. Only one lobster was observed under a small outcrop in the mud bottom plot and none was encountered on the sandy bottom.

An extensive study conducted by Stewart (1970) included a population survey on a 232-m^2 site off Ram Island, Connecticut, in Long Island Sound. The substrate in this area is mud–silt with scattered boulders 61–181-cm diam. The highest average abundance calculated from Stewart's data was one lobster every 9.34 m^2, which is very similar to that of Cobb's results for a broken rock bottom. Stewart also noted that the addition of new niche space to preexisting habitats increased the carrying capacity by almost 50% during his study.

Scarratt's (1968, 1973) long-term study on an artificial reef constructed in the Northumberland Strait describes the development of the flora and fauna over a period of 7 yr. Surveys conducted 2 yr after installation (Scarratt 1968) indicated that lobster biomass was less than that on nearby productive grounds (estimated to be one lobster every 5.63 m^2 with a biomass 12.6 g/m^2). More recent surveys (Scarratt 1973) indicate that the lobster population has increased significantly, yielding one lobster for every 6.45 m^2, with a biomass of 15.1 g/m^2.

The present study confirms that relatively high lobster biomass (up to 74.2 g/m^2) can be obtained with artificial shelter. The abundance (numbers per unit area) for single unit shelters spaced at 122- or 244-cm intervals is similar to that obtained by Scarratt (1968, 1973), and for triple chamber units at 244 cm or single unit shelters spaced at 61- or 30-cm distances, the abundance is greater than that obtained by Scarratt. The rapid rate of occupation of shelter units in this study may be due to the close proximity of resident populations or other local conditions. Except for minor seasonal fluctuations, occupancy seems to have stabilized after about 9 mo.

The effect of intershelter spacing interval on lobster occupancy suggests that the nearest-neighbor distances may be a critical factor in shelter selection. The frequency of multiple occupancy in the single-chamber shelters suggests that the critical nearest-neighbor distance for juvenile lobsters was not reached and probably lies within the dimensions of the shelter itself. Shelter spacing at intervals of 30 and 61 cm did result in increased sediment transport out of the matrix thus sinking the matrix block as a unit.

The physical stability of shelters on the seabed was significantly influenced by the orientation of the shelters. When the shelters were placed on the seabed, which was composed of noncohesive sediments, they disturbed the dynamic stability of the bed. The local velocity around the object shelter increased above the mean flow velocity, which caused a greater sediment transport capacity. The resultant scouring action on the shelter was a function of the flow velocity and the shelter geometry. Jones (1974), using a unidirectional flow water channel with a movable sand bed, examined the influence of current velocity, sediment type, and shelter orientation on the local scour characteristics of shelters. His results confirmed observations that shelters oriented with openings perpendicular to flow were least effected by scour.

Based on almost 7 yr of observation of his reef, Scarratt (1973) indicated that parts of the reef were thicker than necessary and that the same volume of material spread over a greater area might support a greater population of lobsters. Despite careful efforts at site selection (including a geological survey), parts of the reef

settled or were inundated by sand which indicated that adequate reef substrate might be limited. Scarratt (1973) suggested that alternative material sources, placement methods, and configurations must be found before reef construction for lobsters can be considered a sound economic investment. Although the development of small scale commercial lobster fisheries on a large reef has been described (Briggs and Zawacki 1974), these reefs may not be justifiable on a cost benefit basis (Scarratt 1973), unless other uses such as sport fisheries can be developed. It is important to consider all the costs involved, including the cost of material, necessary processing, transport, and deployment. As energy and raw material costs increase, items such as worn-out tires and discarded automobiles may become less feasible as reef materials (Anon. 1974).

The use of low profile unit shelters that have been designed specifically for the lobster may offer an alternate strategy to the construction of large scale reefs of either natural or scrap materials. If some of the legal restraints are removed, additional uses, such as "extensive" aquaculture, may develop. At present, the shape limitation (size and curvature) of the material (pumice cement) and the requirement of diver deployment restrict the use of such shelters. Investigations to consider alternate materials and deployment techniques are underway.

Jones (1974) has examined the bottom stability of a new hemispherical shelter by using a computer simulation model that theoretically determined the wave and current forces acting on the shelter. Based on this work a new shelter design has been developed and is currently undergoing extensive field testing to refine site selection criteria. Studies designed to evaluate the potential of reefs stocked with lobsters in conjunction with supplemental feeding have also been initiated.

Acknowledgments

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Evidence for the Presence of Molt-Inhibiting Hormone in the Sinus Gland of the Lobster *Homarus americanus*

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Implantation of American lobster (*Homarus americanus*) sinus glands into the ventral hemocoele of the crayfish (*Procambarus simulans*), in which molting has been induced by eyestalk removal, significantly retarded the onset of molt ($P < 0.001$). Implanted animals required nearly twice as much time to molt as controls; implanted animals molted in approximately 15 days and controls in about 8. These findings support the hypothesis that the lobster sinus gland contains a molt-inhibiting hormone.

COUCH, E. F., C. S. DAILY, AND W. B. SMITH. 1976. Evidence for the presence of molt-inhibiting hormone in the sinus gland of the lobster *Homarus americanus*. J. Fish. Res. Board Can. 33: 1623–1627.

L'implantation de glandes sinusaires de homard américain (*Homarus americanus*) dans l'hémocèle ventral de l'écrevisse (*Procambarus simulans*) chez laquelle la mue avait été provoquée par ablation du pédoncule oculaire, retarde de façon significative le début de la mue ($P < 0.001$). Les sujets soumis à une implantation prennent près de deux fois plus de temps à muer que les témoins : environ 15 jours pour les premiers et environ 8 jours pour les derniers. Ces constatations appuient l'hypothèse que la glande sinusaire du homard contient une hormone inhibitrice de la mue.

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IN the past few years the presence of a molt-inhibiting hormone (MIH) in the lobster sinus gland has been questioned by some authors, while others have contended that the hormone exists at this site. In 1951 Donahue stated in a semi-popular report that eyestalk removal caused the lobster to molt sooner. But this assertion was not verified by experimental data. However, in 1973 two experimental papers appeared that supported the thesis that MIH exists in the lobster eyestalk (Sochasky et al. 1973; Rao et al. 1973). Sochasky et al. found that eyestalk removal in adult lobsters caused precocious molting[1] while Rao et al. reported successful molt induction after eyestalk removal in larval stages of *Homarus americanus* (stage 4 and 5).

These studies, however, are in contrast to earlier reports of failure, or at least difficulty, in inducing molt in the lobster. In an article appearing in 1969, Aiken commented that eyestalk removal in lobster has "not been very successful" in inducing molt in *H. americanus*, although he and his coworkers (Sochasky et al. 1973) now have amended this view and believe that under certain defined conditions molt induction can occur. Earlier, Travis (1951) mentioned that eyestalk removal failed to induce molt in lobsters and finally in 1972 Flint published studies in which he also reported that the removal of eyestalks from adult lobsters failed to induce precocious molting.

We therefore have addressed the question: Can molt-inhibiting hormone be demonstrated in lobster sinus glands? We have studied the effect of lobster sinus gland implantation on crayfish induced to molt by eyestalk ablation. Our results show that these implants delay molt in the crayfish (*Procambarus simulans*) and therefore support the view that a molt-inhibiting hormone is present in the lobster sinus gland.

[1]Molt and molting in this paper are used synonymously with the more exact term ecdysis. Both words as used here are meant to describe the actual shedding of the old exoskeleton.

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Materials and Methods

American lobsters (*H. americanus*), which served as sinus gland donors, were obtained from the Northeast Marine Specimens Company (P.O. Box 1, Woods Hole, Mass.). Prior to use the animals were maintained in a saltwater aquarium. Both male and female animals weighing between 560 and 1100 g were used. During the time that the lobsters were maintained in the laboratory, they were fed frozen fish 3 times a week.

Crayfish (*P. simulans*) were collected from a small stream near Lake Benbrook in Tarrant County, Texas. Stock animals were maintained in plastic pans and fed either ground beef or fish twice weekly. The animals used in the experiments had been recently collected and in the laboratory for only a week or so before the start of the experiments. The animals were collected in May and early June and the experiments carried out during June and July.

The average cephalothorax length of the crayfish, experimental and control combined, was 2.34 ± 0.043[2] cm, while the individual means of the experimental and control groups were 2.28 ± 0.061 cm and 2.42 ± 0.062 cm, respectively. The control group consisted of 11 males and 12 females and the experimental group 13 males and 6 females. Because of the uneven distribution of the sexes in the experimental group, the *t*-test was applied to determine if any difference in molt induction existed between the sexes. The test showed that the sex of the animal does not affect the molting time ($P > 0.8$ in controls; $P > 0.2$ in experimentals).

Lobsters and crayfish used in the experiments were without gastroliths at the start of the experiment. This insured some uniformity because the absence of gastroliths places the animal in either intermolt or in the very early premolt stage (stage C_4 or D_0 according to Drach 1939). Gastrolith growth has proven unreliable in dividing the substages of premolt but the absence of gastroliths at least insures that the animals are approximately at the same stage. Presence or absence of the gastroliths in both species was determined by x-raying the animals.

Eyestalks were collected from lobsters being used in other experiments. Upon removal the eyestalks were immediately frozen on dry ice; they were then placed in glass vials, sealed, and placed in a deep freeze for storage before use. We found that the seal must be watertight to prevent the eyestalk tissue from dehydrating because it is difficult if not impossible to dissect the sinus gland from dehydrated eyestalks. In two cases, sinus glands were dissected from unfrozen eyestalks. We found, however, that dissection from this fresh material was more tedious than dissection from previously frozen tissue.

The lobster sinus glands were dissected from the eyestalk contents by splitting the eyestalk at its base with fine scissors and gently pulling out the tissue with fine watchmaker's forceps. The tissue was then placed in a pool of crayfish Ringer solution (Van Harreveld 1936) under a dissecting microscope. In indirect light the sinus gland has a bluish opalescent color that is quite distinct from the surrounding ganglionic tissue. This gland was dissected away from the surrounding nervous tissue with a razor blade.

A small hole was made in the second or third abdominal sternite of the crayfish with a metal probe; one sinus gland was then inserted into the abdomen with fine watchmaker's forceps and lodged between the ventral surface of the abdominal muscles and the exoskeleton. The gland was clearly visible after implantation and during the first few days it maintained its bluish opalescence. Control animals received the same surgical treatment but no sinus gland was inserted.

Bleeding was arrested by Avitene®,[3] a microcrystalline collagen hemostat. The animals were kept in the air for 10 min after implantation before being returned to water.

After sinus gland implantation the crayfish eyestalks were removed to induce molting. To reduce trauma, one eyestalk was removed the day following implantation and the second was removed the next day. Bleeding was again controlled with Avitene®. Days to molt were counted after removal of the second eyestalk. Molting in the controls was induced in the same way.

Eyestalks were removed with a razor blade and after the application of Avitene® the animals were not immediately returned to water but were left out in the air for about 10 min to aid in blood coagulation.

After the operation the animals were placed in individual styrofoam cups containing tap water. The animals were checked daily for molting and the water was changed if it had become turbid. The animals were not fed during the experiment.

Results

The eyestalkless crayfish that had been implanted with one lobster sinus gland took nearly twice as long to molt as the controls (Table 1). The difference between the mean of the two groups was significant ($P < 0.001$) by the *t*-test. Figure 1 shows a plot of the percentage of animals undergoing ecdysis vs. time in days. There is a clear difference between the curve of the control and experimental group. By day 11 all the controls but only 15% of the experimentals had molted. The median of the control group was 8.5 days and the experimental 14 days; these values were nearly the same as the mean value of each group.

The time required to molt for males and females was compared within the control and experimental group. In both groups no significant difference was found between sexes ($P > 0.8$ in

[2]Value is the SE of the mean.

[3]Obtained from Alcon Laboratories, Fort Worth, Texas, USA.

TABLE 1. Delay of molt in eyestalkless crayfish by lobster sinus gland implants. Values represent mean ± SE of the mean. Numbers in parentheses indicate the number of animals in each group. The *P* value of the difference between control and implanted group was calculated by the *t*-test.

Days to molt		Statistical analysis
Control	Implanted	
8.04±0.34(23)	14.89±0.92(19)	$P < 0.001$

controls; $P > 0.2$ in experimentals). Also, the delay in molt by sinus gland implantation was not related to the size of the recipient animal. The median length of the cephalothorax in the experimental group was 2.38 cm. When animals with cephalothorax lengths above and below the median were compared by the *t*-test, no difference was found in the time required for them to molt ($P > 0.6$).

Finally, statistical tests were made to check possible differences in the potency of the sinus glands implanted. Nearly all the sinus glands implanted had been frozen for some length of time.

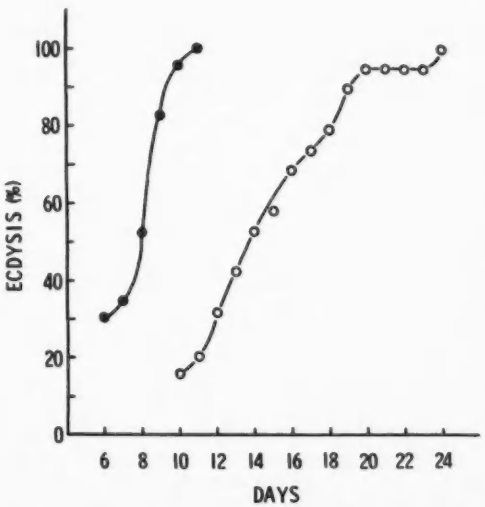

FIG. 1. Effect of American lobster (*Homarus americanus*) sinus gland implantation on molt induction time in the crayfish, *Procambarus simulans*, after eyestalk removal. Eyestalks were removed from 23 control animals (●) and 19 experimental animals (○). Prior to eyestalk removal the experimental group was implanted with one lobster sinus gland. The sinus gland implant caused a significant delay in ecdysis.

However, two experimental animals received fresh unfrozen sinus glands. They molted in 13 and 15 days. Although admittedly the sample is small, when time to molt after fresh sinus gland implantation is compared to frozen, no significant difference is seen ($P > 0.9$). A better sampling was possible when glands frozen for 72 days were compared to those frozen for 4 and 6 days. Six sinus glands had been in the deep freeze for 72 days while another group of 11 sinus glands had been frozen 4 and 6 days. When the ability of the sinus glands frozen 72 days to retard molt was compared to the group that had been frozen only 4 or 6 days, no significant difference was seen ($P > 0.6$). Therefore, the factor in the sinus gland that retards molting seems to be rather stable.

Discussion

It is now generally accepted that the crustacean eyestalk contains a hormone that inhibits molt (Passano 1960). This concept stems from the work of Brown and Cunningham (1939), Abramowitz and Abramowitz (1940), and Passano (1953) who have shown that removal of eyestalks accelerates molting. These contributions really constitute the rediscovery of the same effect that was earlier described in *Uca* by Zeleny (1905) and later in the crayfish *Astacus* by Megušar (1912). Passano (1953) demonstrated that it is the neurosecretory cells of the medulla terminalis of the eyestalk that is the true source of the MIH and the sinus gland itself is but a collection of neuro-secretory cell axonal endings which discharge their contents into a blood sinus. These findings in crayfish and crabs had been believed generally true for all Crustacea, but rather recent work on the lobster (Flint 1972; Aiken 1969) has cast some doubt upon this premise. Aiken in 1969 remarked on the difficulties encountered when attempting to induce molting by eyestalk removal in *Homarus*. However, he and his colleagues now seem to be of the opinion that molt induction is possible in the lobster under certain conditions (Sochasky et al. 1973). Flint (1972), however, stated that he felt molt induction by eyestalk removal in *Homarus* to be impossible. He presented data in which six adult animals lacking eyestalks failed to molt. Therefore conflicting results have appeared in the literature.

The data from our present study support the contention that MIH is contained in the lobster sinus gland. We have shown that lobster sinus glands when implanted into crayfish will significantly retard molt in eyestalkless animals. We

believe that these observations furnish at least indirect evidence that a functional MIH exists in the lobster.

However, we recognize that the data we have gathered is concrete evidence that a factor in the lobster sinus gland retards crayfish molting but it does not prove that this factor (presumably MIH) functions under physiological conditions in the lobster. MIH may be released from other sites in the animal. However, when placing these results in the context of the findings by a number of authors that eyestalk removal causes an acceleration of molt in *Homarus*, at least under proper conditions (Rao et al. 1973; Sochasky et al. 1973; Gagosian et al. 1974), we feel that the sinus gland probably contains MIH and the animal probably uses it to regulate its molt cycle.

This issue could be addressed directly if lobster sinus glands were implanted into eyestalkless lobsters. However, several technical problems have caused us to postpone this experiment and pursue the simpler crayfish experiment first. One problem, and a major one, is the lack of exact knowledge of all the parameters that affect molt induction in the lobster. Sochasky et al. (1973) are working on this problem and have defined some of the necessary conditions for molt induction; but to date not all these conditions are known and many of the factors remain obscure. An additional complication is the length of time needed to induce molt (when successful) in the lobster. Sochasky et al. report that eyestalkless lobsters molt in approximately 60 days; this is in general agreement with unpublished observations made in our laboratory. Therefore, it would seem unlikely that the sinus gland, a structure made up principally of neurosecretory cell endings, would survive such a length of time. Perhaps this difficulty could be overcome by multiple implantations.

The variance was considerably greater in the experimental group than in the control (control variance = 2.37; experimental variance = 15.10). The source of this difference is not known but variation in MIH content among the implanted sinus glands is a possible cause of the observation. This is true even though the donor animals were in general approximately the same size. Furthermore, some of the glands had been stored in a deep freeze for 72 days while others had been in storage less than 6. Possibly, loss in potency during storage could account for the differences. But the statistical test run between those frozen 72 days and those frozen only 4 or 6 days showed no significant difference in inhibiting molt. In fact both groups were not significantly different from the molting time produced by the implantation of fresh unfrozen sinus glands. However, the latter comparison must be taken with some reservation due to the small sample size of the unfrozen implants.

Rao (1965) suggested that an MIH he isolated from the eyestalks of the crab *Ocypode macrocera* is a peptide. Our experiments have shown MIH activity to be retained after 72 days when eyestalks are frozen; this suggests that the MIH may be a rather small molecule because of this stability.

Therefore, the findings presented in our implantation studies combined with evidence accumulating from studies in other laboratories strengthens the view that MIH does exist in the lobster eyestalk.

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An Inexpensive Tag for Short-Term Visual Tracking Studies

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LEAMAN, B. M. 1976. An inexpensive tag for short-term visual tracking studies. J. Fish. Res. Board Can. 33: 1628–1629.

The construction of an inexpensive tag for visual tracking studies is described. The results of field evaluation of the tag are presented and discussed in relation to previous tags and other tracking methods. Advantages of the tag are listed.

LEAMAN, B. M. 1976. An inexpensive tag for short-term visual tracking studies. J. Fish. Res. Board Can. 33: 1628–1629.

Nous décrivons comment peut être construite une étiquette peu dispendieuse pour des études de dépistage à vue. Nous donnons les résultats de l'évaluation de l'étiquette sur le terrain, et nous les analysons en relation avec d'autres étiquettes et méthodes de dépistage. Nous énumérons les avantages de l'étiquette.

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THE study of fish movements has reached a high degree of sophistication in recent years with the use of sonic tags and multiple receivers, such as those employed by Hasler et al. (1969). These systems possess a high degree of accuracy but they remain relatively expensive and their performance decreases in areas of water column occlusion or turbulence, such as nearshore regions in marine and limnetic environments.

One alternative to the sonic tag has been the visual-type tag combined with in situ observation (Heard and Vogele 1968). Constant direct observation of the study fish is required in the use of this type of tag; loss of visual contact can create significant problems in the relocation of the study fish.

This note describes a highly visible, inexpensive tag that allows tracking of fish movements without direct visual contact with the study fish and furthermore, gives an increased ability to locate the fish if such contact is desired.

Description and construction — The tag consists of a standard nylon anchor tag (FD-67, Floy Tag Mfg. Co., Seattle, Wash.) to which is heat fused a length of 5-mm (ID) glass tubing. The tubing is then filled with powdered sodium fluorescein dye and capped with either quick-drying epoxy glue or silicone sealant (Fig 1).

Field evaluation and discussion — The tag was used in a study of the black rockfish, *Sebastes melanops*, and its relationship to kelp beds (*Macrocystis integrifolia*) in Barkley Sound, B.C. Fish were tracked to determine their diel patterns of distribution and the associated utilization of the kelp bed as a habitat.

Fish were captured using monofilament gillnets and anesthetized with M.S. 222 (ethyl *m*-aminobenzoate methanesulfonate). The fluorescein tag was inserted at the base of the dorsal fin, with or without a regular tag, and the fish allowed to recover. The epoxy or silicone cap of the tube is removed immediately prior to release. It is possible to track fish either from the surface (water clarity permitting) or in the water (using SCUBA) by following the trail of dye that diffuses from the tag on the swimming fish. Diffusion of the dye also occurs while the fish is stationary such that individuals hiding in rock crevices can be located. The duration of the tag's effectiveness is a simple function of the amount of dye contained (thus, tag length or diameter). A 55-mm tag lasts approximately 5 h. The trail of dye remains visible in the water from 30 s to 2 min, depending on water clarity and turbulence.

The tag was used on six fish (120–170 mm)

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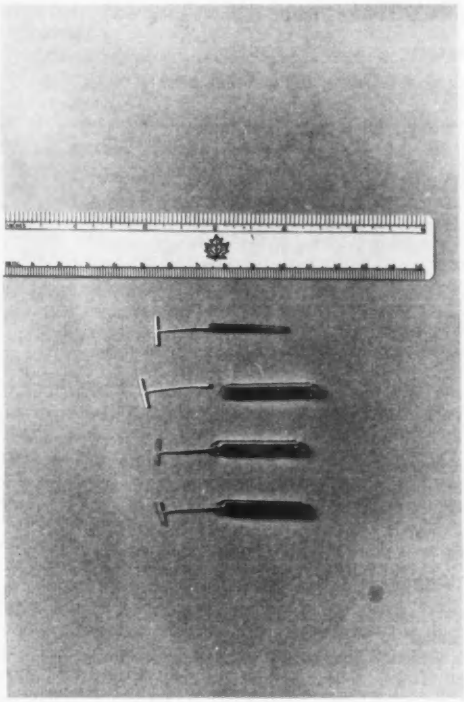

FIG. 1. Construction details of the fluorescein tag. Top to bottom: basic nylon anchor tag; nylon anchor and glass tubing; tubing heat fused to anchor; complete tag filled with fluorescein dye and plugged with silicone sealant.

during May–August 1974, and on five fish (125–200 mm) in August 1975. Use of the fluorescein tags did not appear to affect mortality compared to that of fish tagged with regular tags, as all fluorescein tagged fish were observed >15 days after the fluorescein was exhausted. One 130-mm individual was observed 125 days after tagging. Fish tagged with the fluorescein tag did not display any obviously aberrant behavior, once they had recovered from the initial shock of tagging. Fish with this tag were observed several times within aggregations containing both untagged fish and fish tagged with regular anchor tags.

Fluorescein dye has previously been used in tracking studies by Hasler and Henderson (1963). The tag used by these investigators incorporated a timing device that released a fluorescein pellet producing a large surface stain, and was thus a "two-point" tracking device. The present tag permits continuous tracking and a greater resolution of fish movements.

The major disadvantage of the tag is that only one or possibly two trackings can be pursued simultaneously by one investigator. Advantages of the tag include: low cost, adaptability to environmental situations where sonic tags are ineffectual or impractical, high visibility combined with no apparent increase in mortality over normal tagging, and elimination of the necessity of maintaining visual contact with the study fish and the possible concomitant behavioral reactions.

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Analyses of Gastric Emptying in Bluegill (*Lepomis macrochirus*)

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EL-SHAMY, F. M. 1976. Analyses of gastric emptying in bluegill (*Lepomis macrochirus*). J. Fish. Res. Board Can. 33: 1630–1633.

Bluegill (*Lepomis macrochirus*) fed a single meal averaging 111.6 mg dry wt (2.19% body wt on a wet fish and food basis) showed an average of 60 mg (54%) of the meal remaining after 8 h of digestion compared to 71 mg (59%) of an equivalent amount of food (119.6 mg or 2.04% body wt) fed in two consecutive meals. Fish fed a single meal averaging 167.2 mg (2.74% body wt) showed an average of 41% of the meal remaining 12 h after feeding, while fish fed three consecutive meals totaling 140.3 mg (2.51% body wt), showed an average of 47% of the food intake remaining 12 h after they were first fed. Two statistical models — an exponential and a multiple regression — relating food digested to meal size and time of feeding were developed. Both statistical models, when based on results of fish fed single meals, failed to predict values comparable to those observed for bluegill fed multiple meals.

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Chez les crapets à oreilles bleues (*Lepomis macrochirus*) nourris une seule fois à raison de 111.6 mg en moyenne (poids sec) (soit 2.19% du poids vif du poisson compte tenu du poids humide de la ration), on a remarqué que, après 8 h de digestion, la quantité moyenne d'aliments non digérés correspondait à 54% de la ration alimentaire (60 mg), alors que chez les poissons nourris deux fois de suite les aliments non digérés représentaient 59% (71 mg) de la ration alimentaire (119.6 mg ou 2.04% du poids du poisson). On a également remarqué que, chez les poissons nourris une seule fois à raison de 167.2 mg en moyenne (2.74% du poids du poisson) 41% de la ration alimentaire demeurait dans l'organisme, 12 h après l'ingestion et que chez ceux qui avaient consommé trois rations alimentaires consécutives pesant au total 140.3 mg (2.51% du poids du poisson) cette fraction était de 47%. On a conçu deux modèles statistiques — un exponentiel et un à régressions multiples pour établir une relation entre, d'une part, la quantité d'aliments digérés, et, d'autre part, le poids de la ration alimentaire et la durée de la digestion. Ces modèles, tous deux fondés sur des résultats obtenus avec des poissons nourris une seule fois, n'ont pas réussi à prédire des valeurs comparables aux résultats observés chez les crapets à oreilles bleues, nourris plus d'une fois.

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STUDIES to quantify food consumption rates have been conducted by Kitchell (1970), McComish (1970), and Baumann (1972). Requisite for most of these studies was knowledge of the rate of gastric evacuation (Pandian 1967; Magnuson 1969).

Windell (1966) and Kitchell and Windell (1968) reported an increase in meal size was accompanied by an increase in the amount of food digested per unit of time. However, Barrington (1957) suggested smaller meals were evacuated faster than larger meals. In another case, food passage rates were related to the food most recently ingested (Dawes 1930).

Recent studies on sockeye salmon (*Oncorhynchus nerka*) (Brett and Higgs 1970) and cod (Tyler 1970) indicated that the digestion process can be characterized with an exponential regression, i.e. the amount of food digested per unit of time is proportional to the amount of food present (meal size). Tyler (1970) attempted to test this hypothesis by feeding sequential meals but was unable to draw definitive conclusions.

In the present paper, the exponential hypothesis was tested by increasing the meal size in a carefully controlled experiment. Two simple statistical models were developed to examine the relationships between meal size, food digested, and time of feeding for bluegill (*Lepomis macrochirus*) fed single and consecutive meals.

Materials and methods — Bluegill averaging 135 mm total length (range 116–160 mm) and 40 g wt (range 20–67 g) (Table 1) were collected in June 1971 by bottom otter trawl from Lake Wingra in Madison, Wisconsin. Seventy fish were acclimated to a water temperature of 25 ± 1 C in a holding tank (25 cm deep and 2 m in diam) for a period of 3–4 wk before the beginning of each experiment. Fish were fed ad lib. during the acclimation period on oligochaetes (*Lumbricus rubellus*) cultured in the

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TABLE 1. Lengths, weights, meal sizes, and acclimation periods of bluegill (*Lepomis macrochirus*) used in all experiments.

Expt	Acclimation period (*days*)	No. fish[a]	Total length (*mm*)		Wet wt (*g*)		Meal size (*mg dry wt*)	
			Range	Mean	Range	Mean	Mean ± 2 SE	Mean % body wt
I	26	9	116–145	129	19.6–45.1	36	68.4 ± 10.1	1.07
II	24	7	120–147	132	25.4–45.3	36	111.6 ± 11.6	2.19
III	21	8	125–143	133	28.8–43.9	39	119.5 ± 12.4	2.04
IV	28	8	130–148	136	35.0–56.0	42	167.2 ± 15.2	2.74
V	22	7	134–160	144	40.6–67.4	44	140.4 ± 10.2	2.51

[a]Fish that did not feed well were excluded from analysis.

laboratory. To circumvent errors arising from variations in water content of food materials and liquid buildup in stomachs, wet weights of food were converted to dry weights in all experiments by drying eight subsamples of worms of known weights at 85 C for 48 h. A conversion factor based on average wet weight to dry weight ratio was used (Windell et al. 1969).

Experiments were conducted in a tank divided into nine compartments separated by perforated partitions. Each compartment was aerated and held at 25 ± 1 C. After acclimation and prior to an experiment, one fish was transferred to each compartment. Fish were starved for 48 h before each experiment to allow stomachs to empty. Worms were also denied food for the same period. Fish in each experiment were fed a known ration at a predetermined time(s) and killed at the end of each experiment; fish that did not feed well were excluded from analysis. Food remaining in the stomachs was collected, dried at 85 C, and weighed. Mean lengths, weights, number of fish analyzed, meal size, and acclimation periods for experimental fish are given in Table 1.

Five experiments (I–V) were conducted. In experiment I, fish in all compartments were offered oligochaetes at an average amount of 68.4 mg dry wt (range 39–93 mg). Four hours after feeding, all fish were killed.

In experiment II, fish in all compartments were offered oligochaetes at an average amount of 111.6 mg dry wt (range 84–141 mg) and were killed 8 h after they were fed. In experiment III, bluegill were fed oligochaetes at an average amount of 57.2 mg dry wt (range 41–70 mg). Four hours later they were offered another meal of worms averaging 62.3 mg dry wt (range 39–87 mg) for a total of 119.5 mg dry weight. As in experiment II, 8 h after the first feeding the fish were killed.

In experiment IV, fish were offered a single meal averaging 167.2 mg dry wt (range 129–198 mg) and were killed 12 h after feeding. Fish in experiment V were fed three consecutive meals at 4-h intervals. The first, second, and third meals averaged 49.4 mg (range 44–58 mg), 48.1 mg (range 35–61 mg), and 42.9 mg (range 34–57 mg), respectively. This group also was sacrificed 12 h after the first feeding.

Results — In experiment I, an average of 32% of the initial food intake had left the stomachs after 4 h. This represents an average dry weight digested of 21.7 mg.

In experiments II and III, average dry weights of food digested after 8 h were 46 and 41% of the total food intake, respectively. The digestion rate of fish fed two consecutive meals was slightly lower than for fish fed a single meal. The difference in the percent of food digested by the two groups was not significant ($t = 0.33$; $P \leqslant 0.05$). No significant difference existed between mean size of fish in the two experiments ($t = 0.90$; $P \leqslant 0.05$). The difference between average wet weight of fish in experiments II and III was 3 g (Table 1).

Fish in experiment IV had digested 59% of a single meal after a 12-h period, while fish fed three consecutive meals (experiment V) digested 53% of the total food intake in the same period. Thus, as in the case of experiments II and III, fish fed three consecutive meals showed a higher proportion of the meal remaining than fish fed a single meal of an amount equivalent to the three meals combined. The difference between mean percent weights of food digested for the two groups was not significant ($t = 0.84$; $P \leqslant 0.05$). The difference in fish size between the two groups was 7 g, which was also not significant ($t = 1.72$; $P \leqslant 0.05$).

Models — Two statistical models were developed to describe the digestion process. The models were based on results obtained from the single meal-feeding experiments.

In Model I, it was assumed meal size does not influence the rate of gastric evacuation, i.e. the percentage of food digested per unit time is similar for different size meals. Model I is based on results of experiment IV, where fish were fed a single meal and killed 12 h after feeding. Amounts of food digested 4 and 8 h after feeding

TABLE 2. Dry weights (milligrams) of food ingested (I), food remaining (R), and cumulative food digested (CD) at different times after feeding single (S) and multiple (M) meal to bluegill.[a]

	4 h after feeding					8 h after feeding			12 h after feeding	
	I		R		I	R		I	R	
	S	M	S	M	M	S	M	M	S	M
	168	44	114.1	29.9	35	90.7	46.4	34	49.3	53.3
	149	49	101.2	33.3	50	80.5	58.7	49	62.2	52.0
	152	44	103.2	29.9	61	82.1	62.2	24	50.5	43.9
	129	52	87.6	35.3	40	69.7	54.4	57	70.1	98.6
	198	50	134.4	34.0	60	106.9	65.2	44	91.1	40.8
	192	49	130.4	33.3	45	103.7	55.7	47	64.1	84.3
	176	58	119.5	39.4	46	95.0	61.6	45	79.7	85.6
	174		118.1			94.0			76.0	
Mean	167.3	49.4	113.6	33.6	48.1	90.3	57.8	42.9	67.9	65.5
CD (% *dry wt*)			32	32		46	41		59	53

[a]Three fish were excluded from analyses because they did not feed well.

were extrapolated from experiments I and II (single meal experiments), respectively (Table 2). That is, 113.6, 90.3, and 67.9 mg dry wt of food remained in the stomachs 4, 8, and 12 h, respectively, after a single meal of 167.2 mg dry wt of food was ingested.

Relationship between food intake and food remaining hours after feeding was best fitted by computer to the exponential equation

$$Y = Y_0 e^{-RT} \quad (1)$$

where: Y = dry weight of food remaining
Y_0 = dry weight of food ingested
T = hours after feeding
R = 0.0724

In Model II, meal size was assumed to alter digestion rate in bluegill. Thus, results obtained from experiments I, II, and IV were used to derive equation 2. Food remaining in the stomachs, time after feeding, and meal size data were used to formulate the following stepwise multiple regression equation

$$Y = 32.22 + 0.244\ Y_0 - 0.285\ T \quad (2)$$

The multiple correlation coefficient of Y, Y_0, and T showed a significance at the 5% level ($r = 0.54$). The two independent variables, Y_0 and T, proved to be of significance, explaining a small, but significant, portion of the variance in Y ($R^2 = 0.33$; $F = 4.31$ with 2 and 22 df). The data were further analyzed by *t*-test to determine if the variation contributed by each variable was significant. The variance attributed to Y_0 was significant ($t = 3.0$; $P = 0.025$). The additional variance due to T was nonsignificant and was thus deleted from the analysis. The new equation

$$Y = 32.22 + 0.244\ Y_0 \quad (3)$$

was used in the calculations.

Model I (exponential) and Model II (multiple regression) were applied to food intake data of fish fed three consecutive meals (experiment V), and the results were compared to the actual values. Food remaining 4, 8, and 12 h after feeding predicted by both models as well as the actual values obtained from the three-consecutive-meals experiment are shown in Fig. 1. Percent cumulative food remaining predicted by the exponential model was consistently higher for slower digestion rate than the observed values. Meanwhile, values predicted by Model II suggest slower digestion in the early hours after feeding was followed by a relatively fast rate of stomach evacuation. At the end of a 12-h period, the exponential model and the multiple regression model showed that averages of 56 and 40%, respectively, of the total food intake remained in the stomachs, as opposed to 47% shown by experimental results. The analysis of variance comparing mean weights of food remaining predicted by Model I, Model II, and the actual values was significant ($F_{2,18} = 4.9$; $P = 0.01$). The difference between mean values predicted by Model I and Model II was significant, but neither model yielded a result significantly different from the actual values (Duncan's new multiple range test).

Discussion — The results presented in this paper show that food was digested faster by bluegill when it was ingested as a single meal rather than as two or three successive meals. This conclusion is not in agreement with previous assumptions about food digestion rates (Dawes 1930;

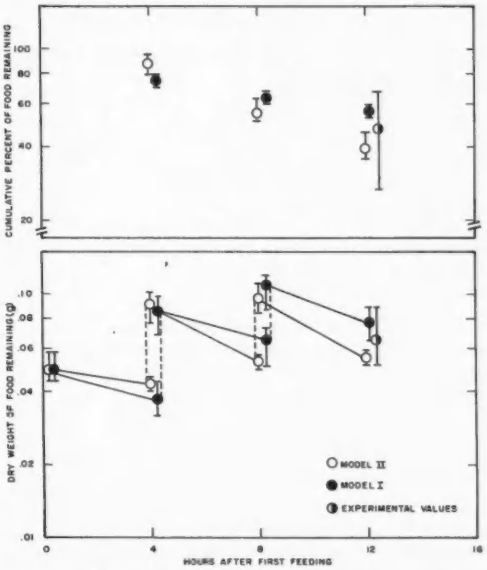

FIG. 1. Cumulative percent of food remaining (*upper*) and dry weight of food remaining (*lower*) hours after feeding as estimated by Model I and Model II and observed values of bluegill (*Lepomis macrochirus*) fed three successive meals. |, ranges; ¦, second and third successive meals.

Barrington 1957). Both the above statistical models failed to predict results comparable to the observed values. Food remaining in stomachs of bluegill 12 h after they were fed three meals was 65.5 mg dry wt (47% of meal size), in contrast to the values predicted by Model I and Model II: 78.6 mg (56%) and 54.6 mg (40%) dry wt, respectively. The variability of the data in some cases has also been reported for other species (Magnuson 1969; Brett and Higgs 1970; Windell et al. 1969).

Norris et al. (1973) reported that a "normal" digestive pattern of pH and enzymatic activity followed the ingestion of a small meal (a glass bead averaging 0.63% body wt). When the meal size increased (two beads averaging 1.26% body wt), a reduction in stomach acidity and enzymatic activity was observed. This was attributed to the depletion in gastric secretion. The enzymatic activity and secretion of gastric acid have not been characterized for fish fed successive meals.

That the digestion process in continuous feeders is more complicated than a simple meal–enzyme relationship is indicated by the present findings. Secretion of gastric enzymes, stimulated by the intake of the first meal after starvation, followed a different course when subsequent meals were ingested before stomachs were cleared. A nearly complete release of enzymes accumulated in starved animals is probably stimulated by the initial meal.

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Variations in Fillet Lipid Content and Some Percent Lipid-Iodine Value Relationships for Large Winter Atlantic Herring (*Clupea harengus harengus*) from Southeastern Newfoundland

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ACKMAN, R. G., AND C. A. EATON. 1976. Variations in fillet lipid content and some percent lipid-iodine value relationships for large winter Atlantic herring (*Clupea harengus harengus*) from southeastern Newfoundland. J. Fish. Res. Board Can. 33: 1634–1638.

Lipid was extracted from fillets of large Newfoundland winter Atlantic herring (*Clupea harengus harengus*) gillnetted in Placentia Bay. In the period January through March percent lipid fell more sharply in females than in males, but lipid-iodine values declined at approximately the same rates. Lipid-iodine values were noticeably higher (about 20 units, maximum values ca. 160) than for the oils produced from fish seined in adjacent waters and commercially reduced. It is proposed that these particular herring are an isolated stock peculiar to Placentia Bay, but that they show certain aspects of lipid biochemistry that are influenced by the reproductive cycle in common with other herring from the Atlantic and Pacific oceans.

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Nous avons extrait les lipides des filets de gros harengs d'atlantique d'hiver (*Clupea harengus harengus*) de Terre-Neuve capturés aux filets maillants dans la baie de Plaisance. Durant la période de janvier à mars inclusivement, le pourcentage de lipides baisse plus brusquement chez les femelles que chez les mâles, mais les valeurs de l'iode lié aux lipides diminuent à peu près au même taux. Les valeurs de l'iode lié aux lipides sont notablement plus élevées (environ 20 unités, valeur maximum ca 160) que celles des huiles provenant de poissons capturés à la senne dans les eaux avoisinantes et extraites commercialement. Nous émettons l'hypothèse que ce groupe particulier de harengs est un stock isolé propre à la baie de Plaisance, mais que ces harengs exhibent certains aspects de la biochimie des lipides influencés par le cycle reproducteur et possédés en commun avec les autres harengs de l'Atlantique et du Pacifique.

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SEASONAL variations in the iodine values of oils from commercial reduction of Canadian Atlantic herring (*Clupea harengus harengus*) were found to vary systematically with time of production in the Nova Scotia summer fishery and the Newfoundland winter fishery (Ackman and Eaton 1970a, b). The biological data on the fish from which these oils were produced were scanty and limited to the date and area of catch, and approximate length. All of these oils would have come from whole, seine-caught fish. Traditionally Newfoundland food herring came from gillnet fisheries. As part of an extension of our knowledge of fatty acids and lipids in this increasingly important human food resource (Jangaard 1973), we have now examined the lipid extracted from fillet (muscle) of large Newfoundland winter herring obtained mostly from gillnet fisheries in and around Placentia Bay, supplemented by other fish obtained from seiners and from fisheries research activities on the south coast of Newfoundland. Fish have been examined on the basis of size, sex, fillet lipid, and lipid-iodine value. Other parameters examined include a limited number of fatty acid studies published elsewhere (Ackman et al. 1975).

Experimental — The majority of the samples, averaging 1 doz fish per lot, were collected during the winter of 1970 by the staff of the Biological Station and by fisheries officers, Department of the Environment, Fisheries and Marine Service, St. John's, Nfld., and shipped frozen to Halifax. The fish were later thawed, weighed, measured (fork length), sorted as to sex, and filleted. One fillet was cut from each fish, pooled for multiple fish samples, and extracted by the chloroform–methanol–water homophase procedure of Bligh and Dyer (1959). The total extract was stripped of solvent under high vacuum while warmed and the iodine value determined by the Wijs method (American Oil Chemists' Society 1972). The sampling data and results of analyses are published elsewhere (Ackman and Eaton 1976) and include data falling outside the January 1–March 31 period which we have examined in detail. Linear regression

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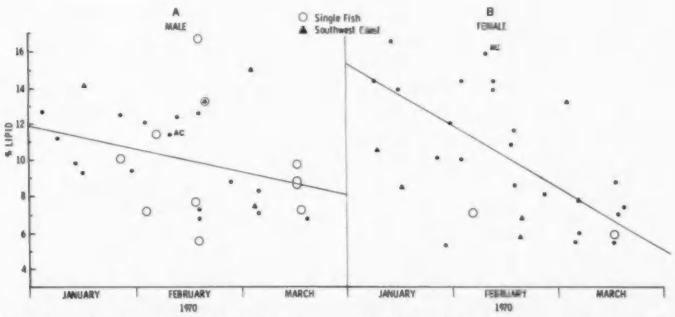

FIG. 1. Seasonal variation in percent lipid in fillets of A, male and B, female Newfoundland winter Atlantic herring (*Clupea harengus harengus*), mostly from gillnet operations in southeast coast bays. Calculation of regression lines includes data for single fish (○) but not the data from samples known to be from the southwest coast (▲). AC indicates a possibly nonconforming sample from Arnolds Cove. The regression formula for A is % lipid = 11.8 + (−0.047) (No. of day in year), and for B, % lipid = 15.4 + (−0.113) (No. of day in year).

lines were determined by computer using the least mean squares method.

Results — After deletion of southwest coast samples for geographical reasons, and samples falling outside the major January 1–March 31 sampling period, plots of percent fillet lipid vs. date of catch (Fig. 1) showed possible linear relationships for both male and female fish which were not apparent from the tabulated data. From the regression lines a much steeper slope for female fish was apparent. The plots of percent fillet lipid and iodine value (Fig. 2), again restricted geographically for calculation of regression lines, also suggested that different relationships exist for male and female fish. The fatter female fish tended to show higher iodine values. Regression lines for the data from the same selected lots of fish for iodine value of lipid vs. date of catch (Fig. 3) showed two virtually parallel lines, the line for females being slightly higher in iodine value. However, curved lines, developed by eye in the fashion previously used for commercial oils (Ackman and Eaton 1970a, b), could be discerned, provided that the group of four points for male fish (Fig. 3A) and six points for female fish (Fig. 3B), all from the southwest coast, were included as in our 1970 reports. The one borderline sample originating in Arnolds Cove is included in all regression lines since it is from the southeast coast. The six samples of mixed sex (Ackman and Eaton 1976) have been omitted from regression lines and discussion.

The iodine values of the fillet lipids from the multiple fish samples examined ranged from 169

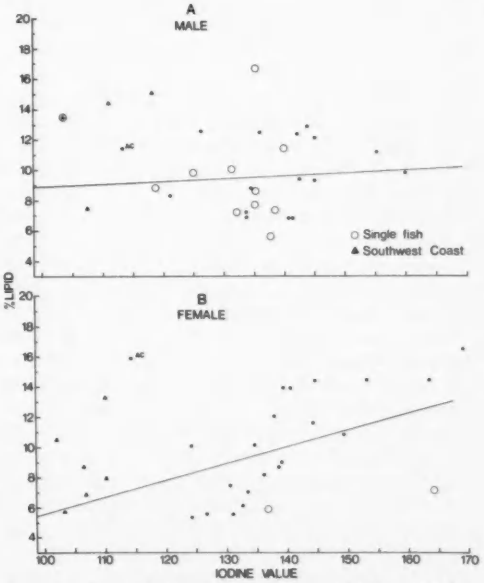

FIG. 2. Interrelationship of percent lipid and iodine values for Newfoundland winter herring as described in Fig. 1. The regression formula for A is % lipid = 7.8 + (0.018) (iodine value), and for B, % lipid = 5.0 + (0.108) (iodine value).

(female, 16.5% lipid, Long Harbour, January 13, 1970) to 103.2 (female, 10.5% lipid, southwest coast, January 9, 1970). Individual fish may not always conform to trends based on examination of several fish as one sample, but single fish analyses, although not taken as typical in dis-

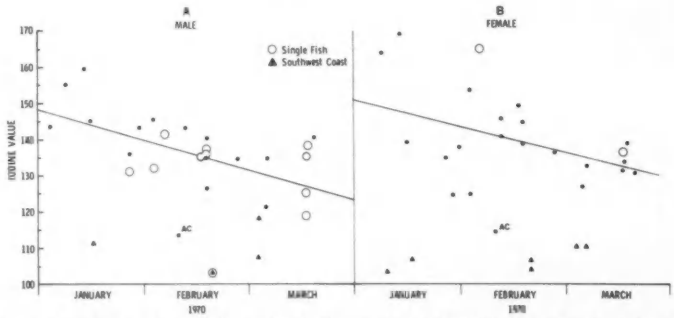

FIG. 3. Seasonal variations in iodine value of lipid for Newfoundland winter herring as described in Fig. 1. The regression formula for A is iodine value = 148 + (−0.254) (No. of day in year), and for B, iodine value = 152 + (−0.266) (No. of day in year).

cussion, are included in the calculation of the regression lines.

Discussion — One of the aims of this study was determination of the fatty acid composition of the fillets from selected fish (Ackman et al. 1975). Accordingly, the Bligh and Dyer method of "lipid" extraction was adopted in preference to recovery of ether-soluble "fat" from dried ground fish as employed by others (e.g. Hodder et al. 1973), since oxidation of the polyunsaturated fatty acids would undoubtedly occur with the latter method. The "lipid" and "fat" results are probably comparable within reasonable experimental accuracy for all values of 10% or more, but for values ranging down to 7% or less, an additional recovery of about 0.5% lipid may be expected from the Bligh and Dyer method (Urdahl and Nygard 1971). This extra lipid represents mostly phospholipids and/or material that would become bound to protein by oxidative polymerization during drying. The factor that limits comparisons with the work of others is that their data are often based on whole fish. Nevertheless, interpretation of our data basically agrees with that for ether extracts of fat and for commercial oils, since in herring the muscle is the principal fat storage site (Flo et al. 1972).

The plots showing seasonal lipid decline (Fig. 1) are essentially similar to those presented by Hodder et al. (1973) for spring and fall spawning whole fish. Hodder et al. (1973) considered that autumn-spawning whole females had slightly less fat than males, while in spring spawners the opposite role prevailed. The fact that herring in Newfoundland waters live on their reserve fat during overwintering is well documented (Hodder 1970; Parsons 1970; Winters 1970; Hodder et al. 1973; see additional references cited by Ackman and Eaton 1970b). Norwegian winter herring show the same characteristics (Villmark 1959); fish taken January 26 averaging 310 g had about 12.6% fat, while those taken on March 16 averaging 310 g had only about 7.3% fat.

The regression lines for the percent lipid vs. time plots (Fig. 1) suggest that female herring initially store more fat in their muscle than do male fish. It is usually thought that fish roe has more lipid than milt (e.g. 4.8% vs. 2.1% in mackerel, *Scomber scombrus*, Hardy and Keay 1972). However, Hølmer (1967) shows lipid content of 3.8% for milt vs. 2.2% for roe in stage V herring and 3.0% for both milt and roe in stage VI or VII herring. The body (including viscera, less gonads) fats are given as male 10.2 and 8.7% and female 16.6 and 13.9% in these respective cases of V and of VI or VII, so the process of muscle fat depletion during gonad maturation may not be as extensive as is sometimes suspected. Flo et al. (1972) show bodies of winter herring (exiscerated, less head) as having fat contents of 6.7% for males and 10.6 for females, with the corresponding gonads having fat contents of 3.6 and 6.5%. This is the more accepted view of higher fat in roe than in milt. The perspective for these fish is slightly different if it is noted that the "bodies" of both males and females have about the same proportion of the total fat in the fish, respectively, 75 and 76%, with the gonad fat as 6 and 12% of the total fat on this basis. Apparently then, to explain that the difference in lipid in our muscle samples during the period January–April could be accounted for by more extensive transfer of fat into roe than into milt would be a superficial view.

During April Danish herring samples (Hølmer 1967) showed changes as follows: male, body lipid 10.2–8.7%, iodine value unchanged at 121;

female, body lipid 16.6–13.9%, iodine value 113–125. The iodine value was 192 for milt vs. 176 for roe in the case of the gonads with 3% lipid cited above. By omitting the southwest coast samples from the calculation of the regression lines, the slope of the line for male samples (Fig. 2A) reversed from an apparently abnormal situation of preferential catabolism of monoethylenic fatty acid to the same sign as for the female samples (Fig. 2B), although in actual fact it is nearly flat. The male relationship is thus similar to, and the female relationship the reverse of, the results of Hølmer (1967). Our particular findings suggest that in males little change in the percent lipid-iodine value relationship takes place in the overwintering period and thus that fatty acids are simply consumed for energy without discrimination. In females, as body lipid is depleted, iodine values decline, probably because high iodine value polyunsaturated fatty acids are transferred to roe. Kondo (1975) finds that in herring muscle (North Pacific fish) totals for fatty acids, grouped by class, remain constant although percent lipid may decline by half.

The seasonal iodine value relationships (Fig. 3A, B) are similar in scatter to those observed for commercial winter herring oils from Newfoundland produced over several years (Ackman and Eaton 1970a, b), although displaced to a higher iodine value by about 20 units compared to the commercial oils produced from the reduction of whole fish, if the mid-March points are taken for comparison. In the earlier study period, 1965–70, year to year differences of up to 15 iodine value units were observed in the commercial oils. The sampling for the latter was usually started in November and carried on into April or May, resulting in the nonlinear overall seasonal pattern described previously (Ackman and Eaton 1970a, b).

The linear slopes for the periods January 1–March 3 are essentially the same for both commercial oils and fillet lipid samples with iodine values falling from about 140 to 125 in this period. Pietrkowski and Trzesinski (1970) working on samples of fillets (skin on) from Baltic herring (taken near Gdansk, Poland) observed that iodine values were 144, 131, 123, 109, 111, and 131 for fat (ether extract) contents of, respectively, 7.3, 8.7, 9.0, 3.7, 4.6, and 17.3%. Apparently in Baltic herring muscle the lowest fat content and the minimum iodine value coincided with spawning, supporting the interrelationships of Fig. 1B, 2B, and 3B for female herring fillets.

We suggest, primarily because of the higher iodine values for fillet fat than for oils produced by the commercial reduction of fish from the southwest coast of Newfoundland, that the gillnet herring examined are a discrete stock with somewhat different fat compositions from the herring commonly exploited by seiners. Fatty acids of fillet fat are essentially the same as those of commercial herring oils. On the other hand, lipids obtained from solvent extraction of whole fish often contain a slightly different mixture of fatty acids than oils expressed from whole fish. Thus Urdahl and Nygard (1971) show that extracts from whole Norwegian herring were averaging 6 iodine value units higher than the corresponding oil produced during reduction of North Sea herring, and 14 units higher than oils from winter herring. Hølmer (1967) shows similar results for two lots of herring, one from August and one from February. Although additional 22:6ω3 and 20:5ω3 in the fatty acids of the extracts would give higher iodine values, the amounts of these acids required to thus elevate the iodine value seem to be excessively large for this simple explanation and we prefer the explanation based on a particular stock of fish.

The only major commercial herring oils of consistently high iodine value (145–150) with which we are familiar are of Alaskan origin (Ackman and Eaton 1970b). The Pacific herring (*Clupea harengus pallasi*) is considered a subspecies of the Atlantic herring (Hart 1973). However, we have noted more 22:1 fatty acid in commercial oils from reduction of Atlantic herring than in oils from Pacific herring (Ackman and Eaton 1975), suggesting some basic difference in environment-related biochemical factors similar to those found between Canadian Atlantic and North Sea sand lance *Ammodytes americanus* (Ackman and Eaton 1971) and capelin *Mallotus villosus* (Ackman et al. 1969; Eaton et al. 1975).

The most obvious choice of parameter for modifying lipids in herring is the reproductive cycle, and a key comparison is provided by Kondo (1974) who observed lower iodine values in flesh lipids of herring from northeastern Kamchatka than Robisch and Gruger (1968) found in Alaskan herring oils (the latter findings are summarized by Ackman and Eaton 1970b). Kondo showed a drop in body lipid for both male and female fish in the immediate prespawning period of April–May (cf. Fig. 1), but found that in the same period, although iodine values for flesh lipids increased by nearly 20 units in the male, they increased only slightly in the female. These increases in iodine value are contrary to the findings in our study (Fig. 3), but apparently the period of sampling the Kamchatka herring corresponds biologically and calendrically to a

period later than for the Newfoundland fish in this study, and therefore to the period of iodine value increase for Newfoundland commercial herring oils shown to occur in April and early May by Ackman and Eaton (1970a, b). Such a difference in spawning etc. may result from factors triggered by light variations as the latitudes of the Newfoundland (48°N) and the Kamchatka (59°N) fisheries are different, and Kondo's results suggest that spawning and associated biochemical changes off Kamchatka occur in late May and early June rather than in April–May. This comparison confirms the desirability of prolonged sampling periods in fish lipid investigations. Moreover, although the stock of Newfoundland herring examined in this study possibly differs in some aspects of lipid biochemistry from other herring taken in Newfoundland waters where fat-iodine values were lower, it clearly follows the same basic lipid metabolic pattern of all spring-spawning herring.

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Life History Notes for a Population of Slimy Sculpin (*Cottus cognatus*) in an Alaskan Arctic Stream

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CRAIG, P. C., AND J. WELLS. 1976. Life history notes for a population of slimy sculpin (*Cottus cognatus*) in an Alaskan arctic stream. J. Fish. Res. Board Can. 33: 1639–1642.

The distribution of a slow-growing population of slimy sculpin (*Cottus cognatus*) extends farther than most fishes into the headwaters of the Chandalar River, Yukon River drainage. The maximum observed age was 7 by which time the fish averaged only 101 mm in length. Most sculpin matured at age 4. The spawning season appeared to be shortly after spring breakup (late May). Fecundity averaged 206 eggs (range 59–339 eggs). The fish fed almost exclusively on stream benthos, chironomid larvae being the most common food item.

CRAIG, P. C., AND J. WELLS. 1976. Life history notes for a population of slimy sculpin (*Cottus cognatus*) in an Alaskan arctic stream. J. Fish. Res. Board Can. 33: 1639–1642.

Une population à croissance lente de chabots visqueux (*Cottus cognatus*) est répartie plus en amont que la plupart des poissons dans les eaux de la tête de la rivière Chandalar, bassin du fleuve Yukon. L'âge maximum observé est 7, alors que les poissons mesurent en moyenne seulement 101 mm de longueur. La plupart des chabots atteignent la maturité sexuelle à l'âge 4. La saison de fraie semble avoir lieu peu après la débâcle (fin mai). La fécondité est en moyenne de 206 œufs (extrêmes de 59–339 œufs). Les poissons se nourrissent presque exclusivement du benthos de la rivière, les larves de chironomides étant l'item le plus communément consommé.

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IN the northern fresh waters of North America, the slimy sculpin (*Cottus cognatus*) is the most widely distributed member of its genus and is virtually the only freshwater sculpin in Alaska that occurs in the Bering, Chukchi, and Beaufort Sea drainages (McPhail and Lindsey 1970; Scott and Crossman 1973). Despite this extensive distribution and the often-mentioned importance of *C. cognatus* as a forage fish, very little is known about its life history, especially for northern populations. The purpose of this report is to describe the growth, maturity, fecundity, and food habits of slimy sculpin in the headwaters of the Chandalar River, an arctic tributary of the Yukon River in Northeastern Alaska. These data are compared to accounts of *C. cognatus* populations in southern latitudes (Van Vliet 1964; Petrosky and Waters 1975).

Methods — During summers of 1972 and 1973, surveys were conducted of fish populations in the headwaters of the Chandalar River (East Fork) (Ward and Craig 1974; Craig and Wells 1975). Slimy sculpin were collected by dipnet, seine, and electroshocker at various mainstream locations between Junjik River and Cane Creek.

Laboratory analysis of specimens included a determination of total length to the nearest millimeter, weight to the nearest 0.1 g, sex, maturity, and stomach contents. Ages were determined by otoliths. Van Vliet (1964) used this method and found that otolith-based ages corresponded closely with ages derived from other bony structures in the same fish.

Description of the study area — The Chandalar River (East Fork) originates in the Brooks Mountain Range and flows south approximately 290 km (180 miles) before entering the Yukon River near Fort Yukon, Alaska. The study area includes only the upper reaches of this stream (Fig. 1).

The Chandalar River shares many characteristics with the larger north-flowing streams in the Brooks Range as described by Craig and McCart (1975). There are small headwater glaciers and several perennial springs, but the principal sources of water are snowmelt and rainfall. The streams flow about 5 mo of the year, beginning in early or mid-May and extending until late September or early October. In the mountain regions, the shallow, braided channels freeze solid in winter except in spring-fed areas. Farther downstream in the foothills region, there is only one deep, meandering channel which does not freeze to the bottom during winter months.

Water temperatures may reach high levels for short periods in the summer months. Maximum recorded

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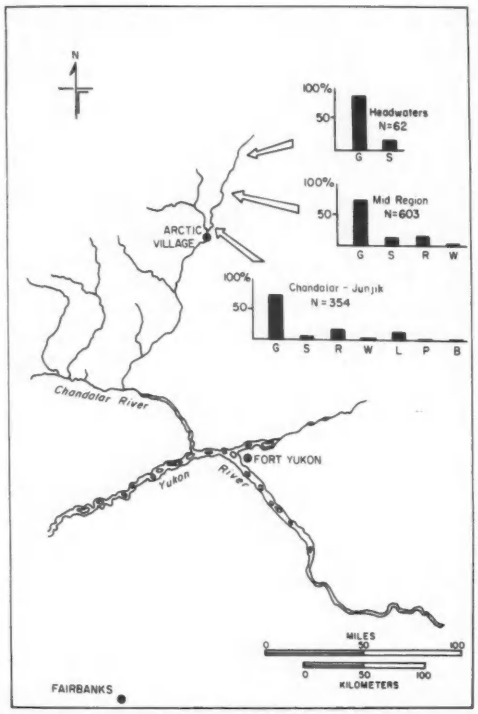

FIG. 1. Chandalar River showing species composition of fishes in the headwater study area. Abbreviations used are: G (grayling), S (slimy sculpin), R (round whitefish), L (longnose sucker), W (broad whitefish), P (pike), and B (burbot).

temperatures were 17.5–20 C in two, small unnamed tributaries in foothill areas but only 11.5 C in mountain areas.

Fish distribution — *Cottus cognatus* has been collected throughout the Yukon River drainage and it is a common and widely distributed species in the upper Chandalar drainage. This sculpin, along with Arctic grayling (*Thymallus arcticus*), penetrates farther than other fishes into headwater areas (Fig. 1). Although the grayling is the predominant fish, slimy sculpin were collected throughout the study area in shallow river channels as well as many headwater tributaries and lakes (Ward and Craig 1974).

Spawning period and fry growth — Since young-of-the-year slimy sculpin were not frequently encountered in the study area, data from the nearby Sheenjek River drainage are mentioned briefly. Newly hatched young-of-the-year, 7 mm long, were found alongside eyed eggs on June 25, 1973 in Monument Creek (water temperature 8 C). By using Van Vliet's calculation for egg incubation time (28 days), it is estimated that the Monument sculpin spawned in late May, 1 wk after spring breakup. Water temperature at that time (May 27) was 3.5 C. In Minnesota this species spawns a full month earlier (Petrosky and Waters 1975).

A sample of 31 young-of-the-year from Old Woman Creek measured only 11–13 mm on August 1, and three fish from the Chandalar River had reached lengths of 19–24 mm by freeze-up (September 26, 1973). These values are markedly smaller than the mean lengths of 45–50 mm attained by young-of-the-year in the Montreal River, Saskatchewan (Van Vliet 1964) and Valley Creek, Minnesota (Petrosky and Waters 1975).

Age and growth — The older Chandalar sculpin also grew exceedingly slowly. Fish aged 1 yr averaged 36.6 mm in length and thereafter grew at an average rate of only 10.8 mm/yr (Table 1). Even by age 7, few fish in the population exceeded 100 mm.

Growth is considerably slower in the Chandalar population than in those described by Petrosky and Waters (1975) for a Minnesota population or by Van Vliet (1964) for three Saskatchewan populations (Fig. 2). As is characteristic of many northern fish populations, the Chandalar sculpins tend to grow more slowly and live longer but reach smaller maximum sizes than fish in the more southern latitudes. For example, the oldest and largest sculpin caught in the Chandalar River was a 7-yr-old male, 104 mm long. In Saskatchewan, *C. cognatus* grew larger than this but they were not as old. The oldest and largest fish Van Vliet collected was a 5–6-yr-old male (127 mm) from the Bow River. Saskatchewan sculpins also weighed much more than Chandalar sculpins (up to 34.3 g vs. a maximum observed weight of 14.1 g).

The following weight–length relationship was obtained for the Chandalar population ($n = 113$; $r = 0.98$):

$$\log_{10}\text{weight (g)} = 2.98 \log_{10}\text{length (mm)} - 4.92$$

Maturity — The age at sexual maturity was similar for both sexes. Some fish were mature at age 3 and almost all had matured by age 4 (Table 1). Age at sexual maturity corresponded closely with a minimum size of 65–75 mm. Van Vliet (1964) found a similar minimum size limit (70 mm) for sexual maturity in a river population of slimy sculpin but, unlike the Chandalar fish, the Montreal River population reached this size in their 1st or 2nd yr of life. Likewise, the Minnesota sculpins were mature by age 2 and some

TABLE 1. Age–length relationships and maturity for slimy sculpin (*Cottus cognatus*) in the Chandalar River.

	Total length (*mm*)				% mature			
Age	N	mean	(range)	SD	N	♂	♀	total
1	32	36.6	(28–44)	4.4	32	0	0	0
2	12	50.8	(45–59)	4.6	12	0	0	0
3	22	65.0	(54–79)	9.3	17	25	11	18
4	33	74.1	(55–87)	7.5	29	93	86	90
5	29	85.6	(74–95)	5.8	28	100	92	96
6	6	94.8	(83–107)	7.9	6	100	100	100
7	3	101.3	(99–104)	2.5	3	100	100	100
Totals	137				127			

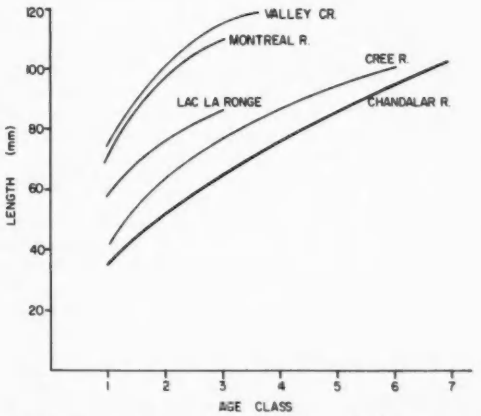

FIG. 2. Comparison of growth rates of slimy sculpin (*Cottus cognatus*) from the Chandalar River with those from Valley Creek, Minnesota (Petrosky and Waters 1975) and three Saskatchewan populations (Van Vliet 1964).

by age 1 (Petrosky and Waters 1975). The slower growing fish in Cree River (Saskatchewan) reached maturity by age 4 (Van Vliet 1964).

All slimy sculpin in the Chandalar River beyond the minimum size of 75 mm possessed gonads sufficiently large to indicate that they would spawn the following springtime, thus suggesting that these fish are annual spawners.

Fecundity — Fecundities for the Chandalar sculpins were lower than Van Vliet's (1964) mean counts for females in the Montreal River (309–1291 eggs) but were similar to those in Lac La Ronge (82–290 eggs). The Chandalar count for females ranging in length from 68 to 99 mm was 206 eggs with a standard deviation of 66.2 (range 59–339 eggs). As observed by Van Vliet, fecundity was positively correlated with length ($n = 22$, $r = 0.95$):

TABLE 2. Frequency of occurrence of food items in stomachs of 132 slimy sculpin ranging in size from 28 to 107 mm, from the Chandalar River.

Food item		% occurrence
Plecoptera	(nymphs)	17
Trichoptera	(larvae)	1
Ephemeroptera	(nymphs)	12
Diptera		
Chironomid	(larvae)	76
Tipulid	(larvae)	15
Empidid	(larvae)	11
Muscid	(larvae)	2
Unidentified		6
Hemiptera	(adult)	1
Unidentified material		14
Rocks		3
Empty		8

$$\log_{10}\text{fecundity} = 4.15 \log_{10}\text{length} - 5.31$$

Sex ratio — As in Van Vliet's (1964) samples, there was no significant difference between the total numbers of males and females in the Chandalar sample ($\chi^2 = 0.45$, $P > 0.05$).

Food habits — The Chandalar sculpins fed almost exclusively on the larvae of stream-dwelling insects. Chironomid larvae, by far the most common food item, were recorded in 76% of the stomachs (Table 2). The remainder of the diet consisted of other dipteran larvae, plecopteran, and ephemeropteran nymphs. Other workers have found a similar reliance on bottom fauna by *C. cognatus* (Koster 1936; Van Vliet 1964; Shallock 1965; Hatfield et al. 1972; Stein et al. 1973; and Petrosky and Waters 1975).

Shallock (1965) suggested that slimy sculpin and grayling might be competitors since they shared many of the same food items in the Chatanika River. While slimy sculpin are re-

stricted to bottom feeding (Van Vliet 1964) and grayling tend to concentrate on stream drift (Vascotto 1970), both fishes, nevertheless, feed on many of the same invertebrates although sometimes at different stages of the invertebrates' life cycle. Similar diets for these two fishes were also noted in the Chandalar River (Craig and Wells 1975), but it remains to be seen whether slimy sculpin and grayling are actually competing for a limited food supply.

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Occurrence of the Woodborer, *Limnoria lignorum* (Rathke) at Amchitka Island, Alaska

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RICHARDS, B. R., AND C. I. BELMORE. 1976. Occurrence of the woodborer, *Limnoria lignorum* (Rathke) at Amchitka Island, Alaska. J. Fish. Res. Board Can. 33:1642–1644.

Three hundred and sixty-one *Limnoria* specimens collected from wood pilings at Amchitka, Alaska in 1971 and 1974 were all identified as *Limnoria lignorum* (Rathke). This is believed to be the first record of the species on Amchitka; the discovery fills a gap in the known distribution between the west and east coasts of the North Pacific Ocean. Female specimens outnumbered males approximately two to one.

RICHARDS, B. R., AND C. I. BELMORE. 1976. Occurrence of the woodborer, *Limnoria lignorum* (Rathke) at Amchitka Island, Alaska. J. Fish. Res. Board Can. 33: 1642–1644.

Un total de 361 spécimens de *Limnoria* provenant de pilotis de bois à l'île Amchitka, Alaska, en 1971 et 1974 ont tous été identifiés comme étant *Limnoria lignorum* (Rathke). Les auteurs

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croient que c'est le premier signalement de l'espèce à Amchitka; cette découverte comble un vide dans la distribution connue de l'espèce entre les côtes occidentale et orientale du Pacifique Nord. Les femelles sont à peu près deux fois plus nombreuses que les mâles.

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DURING 1971 evidence of crustacean marine borer attack was discovered in Constantine Harbor, Amchitka, Alaska (R. G. Fuller personal communication). Because it was generally believed that no marine borers existed at Amchitka, samples of the attacked wood were sent to the William F. Clapp Laboratories for borer identification.

Procedure — Wood samples were removed from pilings supporting Kirilof Wharf, Constantine Harbor, Amchitka, Alaska in August 1971 (Sample 1) and November 1971 (Sample 2) and preserved in 70% ethanol. The dock was constructed from untreated piling in 1942–43. In June 1974, Sample 3 was taken from the ruins of the marine skidway at the head of Constantine Harbor, approximately 1½ km southwest of Kirilof Wharf. The skidway timbers, originally treated with preservative, had interior areas of unpreserved wood at the rusted-out bolt holes which were exposed to open water and borer attack.

Whole borer specimens removed from the wood were microscopically examined and keyed to species (Menzies 1957, 1959; Schultz 1969). A total of 361 specimens were examined: 13 from Sample 1, 71 from Sample 2, and 277 from Sample 3. These specimens were also compared with 45 William F. Clapp Laboratories' Museum specimens obtained from the east and west coasts of North America. Representative specimens from Amchitka have been deposited in the William F. Clapp Laboratories' Museum.

Results and discussion — All specimens from Amchitka fitted the diagnosis of *Limnoria lignorum* (Rathke) given below; this constitutes the first record of the species from Amchitka: branches of uropods dissimilar; exopod small and clawlike, endopod long with apex blunt; flagellum of second antenna with four articles; pleotelson lacking tubercles; pleonal segment five with one medial ridge, pleotelson with one bifurcating ridge on dorsum.

Adult specimens ranged from 2.5 to 5 mm in length, (average approx. 3.5 mm). The lengths are comparable with those found by Kussakin (1963) who reported that *L. lignorum* specimens from Kamchatka, USSR ranged up to 5.5 mm long.

Menzies (1954) found the sexes of *Limnoria* in a 50:50 ratio in populations taken from pilings in San Diego, Calif. In samples from Amchitka females outnumbered the males approximately two to one. The dominant species in San Diego Harbor is *L. tripunctata* (Hochman 1959), and the species in Amchitka is *L. lignorum*. Possibly the difference in sex ratios may be due to differences in species and geographical locations. The sex of the juveniles could not be determined, and the condition of 75 specimens from Sample 3 precluded measurement or sexual determination (Table 1).

Limnoria lignorum has been recorded from Adak, Kodiak, and Sitka, Alaska since 1948 (William F. Clapp Laboratories, Inc. 1952–59). It has been reported from British Columbia (Black and Elsey 1948), Washington, and northern California (William F. Clapp Laboratories, Inc. 1952–59). The United States National Museum collection contains undated specimens of *L. lignorum* from N. Grebnitski, Komandorski Islands. Kussakin (1963) stated that *Limnoria* was collected at the Komandorski Islands, and at Avacha Bay, Eastern Kamchatka, USSR, in 1880. The arc

TABLE 1. Number, sex, and length of *Limnoria lignorum* from Samples 2 and 3.

	Length (*mm*)						
	1.50–2.00	2.50–2.75	3.00–3.50	3.75	4.00–4.50	5.00	Total
Males		2	36	1	21		60
Females		6	45		42		93
Gravid females			8		12	5[a]	25
Juveniles	54						54
Undetermined			22		19		41
Identified only[b]							75

[a]One juvenile in brood pouch.
[b]Poor condition for sex determination or measurements.

formed by the Alaskan Peninsula and the Aleutian Islands extends through the Komandorski Islands. Therefore, the presence of *L. lignorum* on Amchitka should not be unexpected. This report fills a gap in the recorded distribution of the species along the island arc across the North Pacific Ocean.

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Growth Per Molt and Limb Regeneration in the Spider Crab, *Chionoecetes opilio*

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MILLER, R. J., AND J. WATSON. 1976. Growth per molt and limb regeneration in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 33: 1644–1649.

Spider crabs, *Chionoecetes opilio*, were held in the laboratory for observations on carapace width increments and limb regeneration per molt. The merus (the longest limb segment) of autotomized limbs regenerated to 48 and 73% of their full length, irrespective of crab size, on the first and second molt, respectively. Fitting least squares regressions to percentage increase of carapace width per molt (Y) vs. premolt carapace width (X [in millimeters]) gave the following equations: immature males $Y = 40.7 - 0.363X$; immature females $Y = 45.3 - 0.444X$; mature males $Y = 14.2 + 0.051X$; and females' terminal molt to maturity $Y = 14.0 - 0.014X$. Only the slopes for the first two equations differed significantly from zero. Growth per molt decreased with sexual maturity for both sexes and was significantly less for females molting to maturity than for mature males of the same size. Growth per molt for immature females was significantly greater than for immature males, but the difference was slight.

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MILLER, R. J., AND J. WATSON. 1976. Growth per molt and limb regeneration in the spider crab, *Chionoecetes opilio*. J. Fish. Res. Board Can. 33: 1644–1649.

Nous avons fait des observations en laboratoire sur l'augmentation de la largeur de carapace et sur la régénération des membres après la mue du crabe des neiges, *Chionoecetes opilio*. Le méros (le plus long segment) des membres perdus par autotomie est régénéré à 48 et 73% de sa longueur normale, quelle que soit la taille du crabe, lors de la première et de la deuxième mue respectivement. Des régressions de moindres carrés appliquées à l'augmentation en pourcentage de la largeur de carapace par mue (Y) vs la largeur de carapace avant la mue (X [en millimètres]) donnent les équations suivantes : mâles immatures $Y = 40.7 - 0.363X$, femelles immatures $Y = 45.3 - 0.444X$, mâles matures $Y = 14.2 + 0.051X$ et dernière mue des femelles avant la maturité $Y = 14.0 - 0.014X$. Seules les pentes des deux premières équations diffèrent significativement de zéro. La croissance par mue diminue avec la maturité sexuelle chez les deux sexes et est nettement moindre chez les femelles qui muent pour la dernière fois avant la maturité que chez les mâles matures de même taille. La croissance par mue chez les femelles immatures est significativement plus grande que chez les mâles immatures, mais la différence est faible.

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THIS study provides laboratory data on carapace width increments per molt and limb regeneration per molt for the commercially utilized spider crab, *Chionoecetes opilio*.

Several studies on growth of *C. opilio elongatus* in Japan have been published and are reviewed by Ito (1970). Comparisons will be made with the two studies most relevant to our work (Kon et al. 1968; Ito 1970) and with studies on growth of the king crab, *Paralithodes camtschatica*, since good data are available for this species which has a similar growth form to *Chionoecetes* sp. Growth studies on king crabs were facilitated by the development of a tag that is retained through a molt. Although such a tag for *C. opilio* and *C. bairdi* is under development in Alaska, its long-term retention and effects on mortality have yet to be tested (J. F. Karinen personal communication).

Materials and methods — Crabs for laboratory study were collected with a beam trawl or modified king crab traps in the western Gulf of St. Lawrence during the summers of 1968 and 1969. Aboard the vessel crabs were held in refrigerated sea water at 6 C or below, then transferred to insulated refrigerated containers at the dock for the 8-h trip to the laboratory. The habitat temperature in the western Gulf ranges from 0 to 4 C.

In the laboratory crabs were held in flowing sea water at 5 C or below, and about 30‰ salinity. After 7 days, weak and dead animals were removed and the remainder separated into size-groups of 10-mm internals of carapace width. Each crab was measured, weighed, checked for regenerating limbs, and assigned a number by attaching a tag to a walking leg with thread. Crabs less than 30-mm width were held in perforated plastic containers submerged in tanks while larger animals were held in open compartments of tanks. Crabs were held under natural photoperiod and fed to excess every 2nd day on a mixture of ground cod, herring, beef liver, shrimps, and nereid worms. Water temperature was generally kept between 1 and 5 C by using ambient sea water from November through May, and by refrigeration with a slow flushing rate during other months.

After a crab molted and the shell had hardened, measurements were taken on carapace width (with vernier calipers to 0.1 mm), on the length of the merus (longest segment) of any regenerating limb, and on the length of the merus of the corresponding fully grown limb on the opposite side. Measurements were repeated until three consecutive values agreed, usually within 2 mo of the molt.

Limb regeneration — Of the 42 limbs that showed some regeneration, 24 molted from the limb bud stage (first regeneration) and 18 molted from the succeeding stage (second regeneration).

After the first molt 48% of merus length was regenerated and after a second molt 73% was regenerated (Fig. 1). The percentage recovery of merus length did not vary with crab size for either regeneration (i.e. slopes of regression equations in Fig. 1 did not differ from zero, $P > .05$). Also, the above means for percentage recovery did not

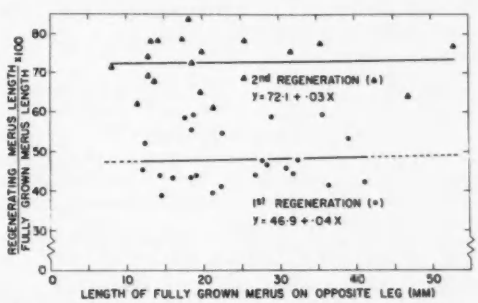

FIG. 1. Regeneration of merus of autotomized limbs of *Chionoecetes opilio*.

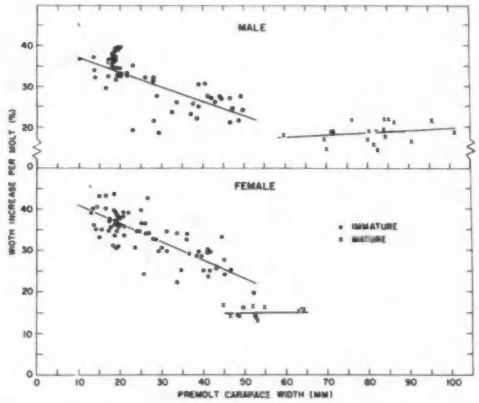

FIG. 2. Percentage increase of carapace width per molt vs. premolt carapace width for *C. opilio*.

differ significantly ($P > .05$) from 50 and 75% which suggests that one-half the difference between premolt merus length and fully grown merus length regenerates with each successive molt. Extending the series to four molts would give 50, 75, 88, and 94% regeneration of merus length.

Regeneration per molt of total limb length has been estimated for juvenile (Kurata 1963) and adult (Niwa and Kurata 1964) king crab, *Paralithodes camtschatica*. Over 7 molts regeneration was 35, 58, 72, 81, 87, 92, and 95% for juveniles, and 29, 50, 65, 75, 83, 87, and 91% for adults. Based on these series, recovery of the difference between regenerating limb length and fully grown limb length was a nearly constant 35% per molt for juveniles and 30% per molt for adults. Edwards (1972) also estimated limb regeneration for juvenile king crabs and obtained a series of 30, 45, 65, and 85% regeneration for the first four molts for a similar average of 36% recovery per molt. All three of these studies obtained their data by picking modes from frequency distributions of percentage regeneration.

The larger the crab the less likely it is to regenerate a limb. None of the crabs over 90-mm carapace width regenerated limbs, even those that had been held in the laboratory for more than a year before molting. At sea few large crabs with regenerating limbs have been found. Most crabs form a scar where the old limb has been autotomized. This scar was reformed after molting in the laboratory.

Nonregeneration is significant to conservation of the resource. Leg loss results when crabs are exposed to sublethal concentrations of crude oil (Karinen and Rice 1974), when fishermen handle subcommercial-sized and soft-shelled (i.e. recently molted) crabs that are returned to the water (personal observation), and when fishermen remove crabs from bottom gillnets set to catch groundfish (Miller and Hoyles 1973). In eastern Newfoundland groundfish gillnets were responsible for an annual loss of 18,000 kg of legs from crabs that survived; however, this was small compared to an annual loss of 876,000 kg of crabs that died from injuries sustained in removing them from gillnets.

Growth per molt — Crabs with old encrusted shells may have reached a terminal molt stage. Of the crabs > 70 mm wide, no crabs with old shells molted in the laboratory ($n = 45$), whereas 33% ($n = 15$) of those with newer shells did. Crabs of all sizes molted in the manner described by Watson (1971).

Percentage growth per molt for immature crabs decreased with increasing crab size for both sexes (Fig. 2; Table 1). Regression equations of percentage width increment per molt vs. premolt width for immature crabs of the two sexes did not differ in slope, but covariance analysis showed that the regression for females had a significantly higher elevation. However, this difference was small: for example, 32.0% increment for females and 29.8% increment for males at a premolt carapace width of 30 mm.

There was no evidence for change in the per-

TABLE 1. Least squares regressions for percentage growth per molt vs. premolt width in millimeters. Data plotted in Fig. 2.

Sex	Regression constants n	a	b	$P(\beta = 0)$	r^2
Immature ♂	55	40.7	−0.363	<0.01	0.53
Immature ♀	76	45.3	−0.444	<0.01	0.61
Immature ♂ & ♀ combined	131	43.4	−0.412	<0.01	0.56
Mature ♂	18	14.2	0.051	>0.05	0.04
Mature ♀	11	14.0	0.014	>0.05	0.01

centage growth per molt with crab size for either mature males or mature females, i.e. the slopes of the above types of plots did not differ significantly from zero (Table 1), although growth per molt was larger for males. Growth per molt for mature males averages 18.4%. Growth of mature females occurs in only one molt since the molt to maturity is the terminal one (Yoshida 1951 quoted in Ito 1970; Watson 1970). The percentage growth for the female molt to maturity averaged 14.8%. Maturity in females was obvious because of a change in the shape of the abdomen (Ito 1970). Maturity in the male is less obvious but, based on the weight of the vas deferens and the presence of spermatophores, Watson (1970) estimated that for male *C. opilio* in the Gulf of St. Lawrence 50% maturity occurred at 57-mm carapace width. This size was used to separate mature from immature males in the lab growth studies.

The decreased growth per molt at sexual maturity for *C. opilio* (Fig. 2) is typical of a variety of crustaceans (Kurata 1962). The difference in growth per molt between juvenile males and juvenile females was not observed previously for *C. opilio* (Kon et al. 1968; Ito 1970), nor is it the general case for other Crustacea (Kurata 1962).

In Fig. 3 the results of five studies on crab growth are compared by plotting percentage growth per molt against molts numbered from the size at sexual maturity. All data for immature crabs are for males and females combined, and data for mature crabs are for males only (Table 2). The data are compared in this way to overcome the problems of differences in the range of crab sizes. Also, by numbering molts from the size at sexual maturity instead of the first stage after metamorphosing to the adult shape, it is not necessary to know the correct number of early molt stages. This data treatment may not be valid for comparing growth of species where a given percentage linear increase (e.g. carapace length or width) does not give a similar percentage weight increase, i.e. where the constants of the weight–length regressions are not similar. This is not a problem in comparing *C. opilio* and *P. camtschatica*, however. The weight–carapace width regression for *C. opilio* from the western Gulf of St. Lawrence is $Y = .00018X^{3.16}$, and weight–carapace length regressions for *P. camtschatica* are $Y = .00037X^{3.14}$ (calculated from Powell 1967) and $Y = .0012X^{2.94}$ (Weber 1967). A 20% linear increase gives 78, 78, and 71% weight increases, respectively, for the above regressions.

The percentages of growth per molt for the three studies on immature *C. opilio* are in reasonable agreement, as are the two studies on immature *P. camtschatica*; however, early molts of the latter clearly have smaller percentage increments than the former (Fig. 3). For the *C. opilio* studies growth ranged from 25 to 40% (this study), 25 to 42% (Ito 1970), and from 31 to 43% (Kon

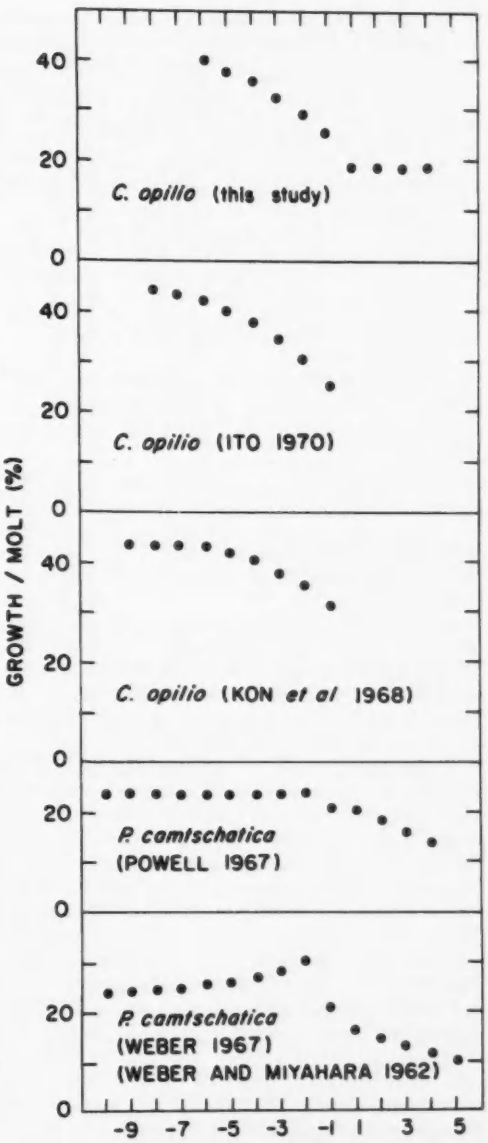

FIG. 3. Percentage growth per molt for *C. opilio* and *Paralithodes camtschatica* with molts numbered from size at sexual maturity.

TABLE 2. Sources of percentage growth per molt data plotted in Fig. 3. Y is percentage growth. X is premolt carapace width for *Chionoecetes* and premolt carapace length for *Paralithodes*.

Sex	Size range (*mm*)	Calculation of % growth/molt	Data base	Source
		Chionocetes opilio		
Immature ♂ and ♀	10–52	Y = 43.5 − 0.412X	Lab. reared	This study
Mature ♂	60–101	Y = 18.4	Lab. reared	This study
Immature ♂ and ♀	7–64	Y = 46.9 − 0.337X	Size freq.[a]	Ito 1970
Immature ♂ and ♀	3–66	Y = 46.4 − 0.303X	Size freq.[a]	Kon et al. 1968
		Paralithodes camtschatica		
Immature ♂ and ♀	10–61	Y = 24	Cage reared[b]	Powell 1967
Immature ♂ and ♀	70–73	Y = 21	Cage reared[b]	Powell 1967
Mature ♂	90–151	Y = 30.0 − 0.112X	Tagged[c]	Powell 1967
Immature ♂ and ♀	7–62	Y = 23.0 + 0.108X	Cage reared[b]	Weber 1967
	60–78	Y = 30	Size freq.[a]	Weber 1967
	78–94	Y = 21	Size freq.[a]	Weber 1967
Mature ♂	94–109	Y = 16	Size freq.[a]	Weber and Miyahara 1962
	110–169	Constant 16-mm increase/molt	Tagged[c]	Weber and Miyahara 1962

[a]Modes of size frequncy distributions constructed from trawl samples.
[b]Reared in cages in the sea.
[c]Recapture of tagged crabs released at sea.

et al. 1968) for the first to sixth molts preceding sexual maturity. For the same six molts the growth of immature *P. camtschatica* was a constant 24% (Powell 1967) or ranged from 21 to 30% (Weber 1967). In the latter study the peak at the second molt before maturity may be due to a change in the source of the data (Table 2).

Although our limited data showed a constant 18% growth per molt for mature male *C. opilio*, other studies on large decapods have more commonly shown decreasing percentage increments per molt for mature males. For the two studies on *P. camtschatica*, growth per molt decreased from 20 to 14% (Powell 1967) and from 16 to 11% (Weber and Miyahara 1962) over four postmaturity molts. Ito (1970) identified modes in a size frequency plot of mature *C. opilio* as molt classes, but these were not significantly distinct to convince us of their validity. Growth per molt in Ito's data decreased from 20 to 6% over five postmaturity molts. In studies on other large decapods, *Pachygrapsus crassipes* (Hiatt 1948), *Cancer magister* (Butler 1961), *Homarus vulgaris* (Simpson 1963), and *Nephrops norvegicus* (Farmer 1973), the percentage growth per molt also decreased with increasing size of mature males. Percentage growth in mature male *Cancer pagurus* (Hancock and Edwards 1967), *Homarus americanus* (Ennis 1972), and *Carcinus maenas* (Walne and Dean 1972) was approximately constant, however.

The three studies on *Chionoecetes* growth per molt appear to be in fair agreement although more data are needed for the sexually mature males. Results on molting frequency from laboratory studies are suspect due to the artificiality of the laboratory environment and due to the reluctance of large individuals to molt in laboratory confinement. Modes in size frequency distributions show molt classes rather than age-classes; hence, unless a population has a synchronized annual molt, ages cannot be assessed from these data alone. Even molt classes modes are typically indistinct for older age-classes of slowly growing species such as *Chionoecetes* sp. (this was the case for western Gulf of St. Lawrence *C. opilio*) since growth per molt is small relative to the accumulated variation in growth per molt and frequency of molt. Development of tags which are retained through molts appears to hold the greatest promise for assessing annual growth in *C. opilio*.

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An Index of Fish Movement with Statistical Techniques for Its Interpretation[1]

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BERGERSEN, E. P., AND T. J. KEEFE. 1976. An index of fish movement with statistical techniques for its interpretation. J. Fish. Res. Board Can. 33: 1649–1652.

A measure of the strength of association between two categorical variables (location of initial marking and location of recapture) is proposed as an index of the extent of fish movement in streams. Confidence intervals and tests of significance for interpretation of the strength of association are presented, along with their development and theoretical justification. The proposed methodology is applied to fish movement data collected before and after pollution-abatement periods in a river in northern Utah.

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BERGERSEN, E. P., AND T. J. KEEFE. 1976. An index of fish movement with statistical techniques for its interpretation. J. Fish. Res. Board Can. 33: 1649–1652.

Les auteurs suggèrent une mesure de la force d'association entre deux variables catégoriques (lieu de marquage initial et lieu de recapture) comme indice de l'amplitude des déplacements de poissons dans les cours d'eau. Ils donnent les intervalles de confiance et les tests de signification permettant d'interpréter la force de l'association, de même que leur développement et leur justification théorique. Ils appliquent la méthodologie proposée à des données sur les mouvements de poissons, cueillies avant et après des périodes de contrôle de pollution dans une rivière du nord de l'Utah.

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CHANGES in water quality can greatly affect many organisms in an aquatic community by altering survival, trophic relationships, or behavioral patterns. Changing environmental conditions are often first manifested in behavioral changes. Because of their relatively high mobility, and ability to avoid or exploit changes in their environment, fish can serve as initial indicators of changing conditions in aquatic habitats; further, a knowledge of fish movements often is useful in identifying subtle changes which might not be readily detected by other means.

Many reports dealing with fish movements are replete with detailed accounts of individual fish expressed in such terms as distance traveled, time between release and recapture, and numbers, with little concern being given to what is happening in the fish community as a whole. Applications of quantitative measures of fish movement are virtually nonexistent. We propose here the use of a measure of association between two categorical variables as a suitable statistic for estimating the extent of fish movement in streams or rivers, and develop confidence interval estimates for the measure.

In stream studies where numerous fish are marked and later recaptured, an examination of the relationship between location of initial capture and location of recapture provides some insight into the extent of movement of the fish population (Table 1). For categorical data of this type, a measure of the strength of relationship between the two categories is provided by a modification (White 1973) of an information measure proposed by Kullback (1959).

Definition of White's measure of association (h) — White's measure of the strength of association between the two categories is defined as

$h = \exp(\overline{w})$, where

$$\overline{w} = \sum_{i=1}^{R}\sum_{j=1}^{C} p_{ij}w_{ij} = \sum_{i=1}^{R}\sum_{j=1}^{C} p_{ij}\log\left(\frac{p_{ij}}{\sqrt{p_{i.}p_{.j}}}\right),$$

and p_{ij}, $p_{i.}$, $p_{.j}$ denote the cell, row, and column proportions, respectively, (i.e. $p_{ij} = \frac{n_{ij}}{n}$; $p_{i.} = \frac{n_{i.}}{n}$; $p_{.j} = \frac{n_{.j}}{n}$). For the 1965–66 data of Table 1, $\overline{w} = -.5652$; thus, $h = \exp(-.5652) = .568$.

As noted by White, the value of h is bounded above by unity and below by $\frac{1}{\sqrt{RC}}$. Consequently a value of h close to 1 indicates a strong relationship between the two categories, whereas a value of h close to $\frac{1}{\sqrt{RC}}$ indicates little or no association. By definition, the ordering of the stations, as well as the measurable distance between stations, is not explicitly accounted for in the index.

Having calculated the sample value of h, an investigator might reasonably be interested in knowing the variability of h; or, more important, he may wish to find a confidence interval for the unknown population measure of association, denoted by H. In either case, knowledge of the sampling distribution of h is required. As with other measures of association for categorical data, the exact sampling distribution of h has not been found. We develop here the approximate distribution of $\overline{w}$ for large sample size n and use that distribution in determining confidence intervals and tests of hypotheses about one or more population H values.

Theoretical development of the approximate distribution of w — It can be shown (e.g. Miller 1966: 216–219) that asymptotically (i.e. as n becomes large) the random vector obtained by "stringing together" the cell proportions from the R × C contingency table, that is

$$\underset{\sim}{p} = (p_{11},\ldots,p_{1C},p_{21},\ldots,p_{2C},\ldots,p_{R1},\ldots,p_{RC})$$

has a (singular) multivariate normal distribution with population mean vector

$$\underset{\sim}{\pi} = (\pi_{11},\ldots,\pi_{1C},\pi_{21},\ldots,\pi_{2C},\ldots,\pi_{R1},\ldots,\pi_{RC})$$

and covariance matrix $\frac{1}{n}\ \Sigma$, where Σ has diagonal elements $\pi_{ij}(1 - \pi_{ij})$ and off-diagonal elements $-\pi_{ij}\pi_{i'j'}$ (either $i \neq i'$ or $j \neq j'$). Thus $\sqrt{n}\ (\underset{\sim}{p} - \underset{\sim}{\pi})$ asymptotically has a multivariate normal distribution with zero mean vector and

TABLE 1. Release and recapture locations of brown trout (*Salmo trutta*), Logan River, Utah, 1965–66 (Matthews 1966) and 1970–71 (in parentheses) (Bergersen 1973). Cell totals indicate the number of fish recaptured at each downstream station.

	Location of previous capture			
	1	2	3	Totals
Location of recapture				
1	$n_{11} = 32(80)$	$n_{12} = 4(2)$	$n_{13} = 0(1)$	$n_{1\cdot} = 36(83)$
2	$n_{21} = 3(1)$	$n_{22} = 21(3)$	$n_{23} = 3(0)$	$n_{2\cdot} = 27(4)$
3	$n_{31} = 2(2)$	$n_{32} = 2(3)$	$n_{33} = 4(2)$	$n_{3\cdot} = 8(7)$
Total	$n_{\cdot 1} = 37(83)$	$n_{\cdot 2} = 27(8)$	$n_{\cdot 3} = 7(3)$	$n = 71(94)$

covariance matrix Σ. Using a theorem from multivariate statistics (Rao 1973: 388–389 or Anderson 1958: 76–77), one can show that $\sqrt{n}\,(\bar{w} - W)/\hat{\sigma}$ is asymptotically distributed as a standard normal variable where $\hat{\sigma}^2$ is given by the matrix quadratic form

$$\hat{\sigma}^2 = \underset{\sim}{\phi}_p' \, \hat{\Sigma} \, \underset{\sim}{\phi}_p,$$

in which $\hat{\Sigma}$ is the sample estimate of Σ and $\underset{\sim}{\phi}_p$ is the vector derivative of $\bar{w}$ with respect to $\underset{\sim}{p}$. In particular, $\underset{\sim}{\phi}_p$ consists of elements ϕ_{ij} in the same order as the p_{ij}'s used in defining $\underset{\sim}{p}$:

$$\phi_{ij} = \frac{\partial \bar{w}}{\partial p_{ij}} = w_{ij} = \log\left(\frac{p_{ij}}{\sqrt{p_{i\cdot}\,p_{\cdot j}}}\right)$$

Thus, $\hat{\sigma}^2$ reduces to the following computational formula

$$\hat{\sigma}^2 = \left(\sum_{i=1}^{R}\sum_{j=1}^{C} w^2{}_{ij} p_{ij}\right) - \bar{w}^2.$$

Approximate confidence interval for the population parameter H — Using the large-sample distribution of w, as developed above, one can derive an approximate $(1 - \alpha)$ 100% confidence interval for the population value W; namely,

$$\left(\bar{w} - Z_{\alpha/2}\frac{\hat{\sigma}}{\sqrt{n}},\quad \bar{w} + Z_{\alpha/2}\frac{\hat{\sigma}}{\sqrt{n}}\right)$$

where $Z_{\alpha/2}$ is the $(1 - \alpha/2)$ percentile of the standard normal distribution. Denoting these limits by W_L and W_U, respectively, for $\alpha = .05$, one can be approximately 95% confident that the interval defined by these two limits contains the true value W. Since H is an increasing function of W, an approximate $(1 - \alpha)$ 100% confidence interval for H is given by simply evaluating the exponential of W_L and W_U; that is, $(H_L = \exp[W_L], H_U = \exp[W_U])$. For the 1965–66 data of Table 1, $\hat{\sigma}^2 = .5396$, the approximate 95% confidence interval for the true W is $(-.736, -.394)$, and thus the approximate 95% confidence interval for the population H is (.480, .674).

Large-sample statistical test of the equality of two population H values — The 1965–66 data in Table 1 were from Matthews (1966) when raw sewage from the town of Logan, Utah was being discharged into the Logan River. The data in parentheses were collected in 1970–71 (2 yr after the abatement of the sewage discharge) from the same sampling locations by similar means (Bergersen 1973). The calculated value of .767 for h for the 1970–71 period indicated a lesser amount of movement in the fish population at this time than during 1965–66, when the value of h was .568. Until now, a statistical test for the significance of differences between h values has not been available.

Our recommended test procedure is to calculate the confidence interval for the W associated with each contingency table and then make one of the following two decisions: i) if the $(1 - \alpha)$ 100% confidence intervals do not overlap, then the difference between the two h values is significant at least at the α level of significance; ii) if the confidence intervals do overlap, perform the following approximate test of significance: calculate Z, where

$$Z = \frac{\bar{w}_1 - \bar{w}_2}{\sqrt{\dfrac{\hat{\sigma}_1^{\,2}}{n_1} + \dfrac{\hat{\sigma}_2^{\,2}}{n_2}}}$$

and reject the hypothesis that the two population H-values are equal if $|Z| > Z_{\alpha/2}$, where $Z_{\alpha/2}$ is the $(1 - \alpha/2)$ percentage point of the standard normal distribution.

Since there was overlap between the approximate 95% confidence interval for the true population H for 1965–66 (.479, .674) and the approximate 95% confidence interval for the

true H value for 1970–71 (.672, .875), the Z statistic was calculated to be −2.71, indicating a significant difference not only at the 5% level, but in fact at the 1% level. The significant change in the two *h*-values indicates a decrease in the extent of movement of brown trout (*Salmo trutta*) in the study area after the pollution abatement.

Although several factors could have contributed to the decreased movement, one of the more plausible explanations can be related to the improvement in water quality. Before the pollution abatement, water quality in the river varied seasonally with changing flow rates and the quantity of sewage discharged. During low water periods in particular, the sewage discharge constituted a fairly high proportion of the river flow below the discharge point, and as a result water quality worsened. Fish below the discharge were apparently forced out of this area, contributing, in part, to the increase in movement. After the pollution abatement, water quality remained reasonably good year-round; consequently, the fish did not need to move out of the river sections that previously had received the raw sewage effluent.

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Biological Notes on *Eupera cubensis* (Bivalvia: Sphaeriidae) from Kansas

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MACKIE, G. L., AND D. G. HUGGINS. 1976. Biological notes on *Eupera cubensis* (Bivalvia: Sphaeriidae) from Kansas. J. Fish. Res. Board Can. 33: 1652–1656.

The occurrence of *Eupera cubensis* (Prime) in Kansas represents a north central range extension. The species appears to be more common in root systems of the water willow, *Justicia americana*, than in riffle areas or backwater areas. Scanning electron photographs are given to illustrate important shell characteristics. The generative performance of *E. cubensis* appears to increase with increasing age up to 3 yr, with as many as 64 larvae, all in the same stage of development, in larger (older) parents.

MACKIE, G. L., AND D. G. HUGGINS. 1976. Biological notes on *Eupera cubensis* (Bivalvia: Sphaeriidae) from Kansas. J. Fish. Res. Board Can. 33: 1652–1656.

La présence d'*Eupera cubensis* (Prime) au Kansas représente une extension de son aire vers le centre-nord. L'espèce semble être plus commune parmi les racines de la carmantine d'Amérique, *Justicia americana*, que dans les régions de radiers ou de remous. Des photographies au microscope électronique à balayage servent à illustrer d'importantes caractéristiques de la coquille. Le pouvoir reproducteur de *E. cubensis* semble augmenter avec l'âge jusqu'à 3 a., un nombre de larves aussi élevé que 64, toutes au même stade de développement, se trouvant dans les parents plus gros (plus âgés).

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THE family Sphaeriidae is represented by three subfamilies, Sphaeriinae, Pisidiinae, and Euperinae, that are distinguishable on the basis of the nature of their siphonal arrangement and development of their embryos. Of the three, Euperinae is the least known with only one species, *Eupera cubensis* (Prime), which has a limited distribution in North America. Only the distribution and systematics of the species has been thoroughly investigated (Heard 1965a). Little or nothing is known of its habitat characteristics, brood sizes, and longevity. The present report is concerned with providing new information on each of these aspects, and with clarifying previous descriptions of the species.

Materials and methods — Both qualitative and semiquantitative collections were made of *E. cubensis* and associated bivalves in the Big Caney River, 2.4 km (1.5 miles) west of Elgin, Chautaugua County, Kansas (37°00′13″N, 96°18′54″W) on July 30, 1975. Semiquantitative samples were obtained by placing a fine-meshed D-frame aquatic net downstream and then disturbing the substrate from an approximate 1-m^2 area of the bottom immediately upstream of the net. The oragnisms and debris were placed in a white tray and only bivalves were picked for 15 min. The procedure was repeated 4 times, once in each of four distinctly different habitats. All habitats were within a 300-m^2 area where the river was 5–7 m wide and approximately 0.3 m deep: the first site was amongst dense growths of water willow, *Justicia americana*; the second in a riffle area where current was swift and the bottom consisted of rocks and gravel; the third in a backwater area where current was sufficient to prevent sedimentation of silt and organic debris; and the fourth in a backwater with a thick layer of silt and organic matter.

Water quality was determined from physical and chemical analyses on six water samples collected approximately every 2 mo in 1974 by Kansas State Department of Health and Environment. Maximum, minimum, and mean values of 18 water characteristics are given in this report.

A linear regression of length on height was done to determine the height–length relationship of the shell in *E. cubensis*. Shell length (millimeters, anterior to posterior) and height (millimeters, top of umbone to ventral edge) were measured on 60 specimens using a vernier microscope (Precision Instruments). The hinge teeth and shell surfaces of representative species were examined and photographed under an Etec Scanning Electron Microscope (S.E.M.) after coating the shells with a thin layer of gold-palladium.

The brood sizes of 60 specimens were determined by dissecting out the left and right inner demibranchs and enumerating the enclosed larvae. The lengths (millimeters) of two to six larvae were determined in each parent. Larvae were recorded as either embryos, fetal larvae, prodissoconch larvae, or extramarsupial larvae: embryos include all developmental stages between the zygote and completed gastrula; fetal

TABLE 1. Water quality characteristics of Big Caney River near collection site of *Eupera cubensis*. All values in milligrams per liter unless indicated otherwise. Means are based on six samples collected approximately every 2 mo in 1974 by Kansas State Department of Health and Environment.

Parameter	Minimum	Maximum	Mean
Alkalinity	120	272	212
Ammonia	0.08	0.48	0.22
B.O.D.$_5$[a]	0.6	1.8	1.1
Calcium	43	99	77
Chloride	14	33	23
Conductivity (μmho/cm)	320	620	495
Hardness, total	128	308	235
Magnesium	5	15	11
Nitrate	0.3	2.8	1.3
Oxygen, dissolved	4.9	12.9	8.8
pH	7.5	8.1	7.9
Phosphate, total	0.15	0.97	0.34
Sodium	10	21	16
Sulfate	11	32	25
Temperature (*C*)	4	26	15
Turbidity	6	130	40
Bacteria (no./100 ml)			
Total coliform	5	2100	365
Fecal coliform	5	500	90

[a]5-day biochemical oxygen demand.

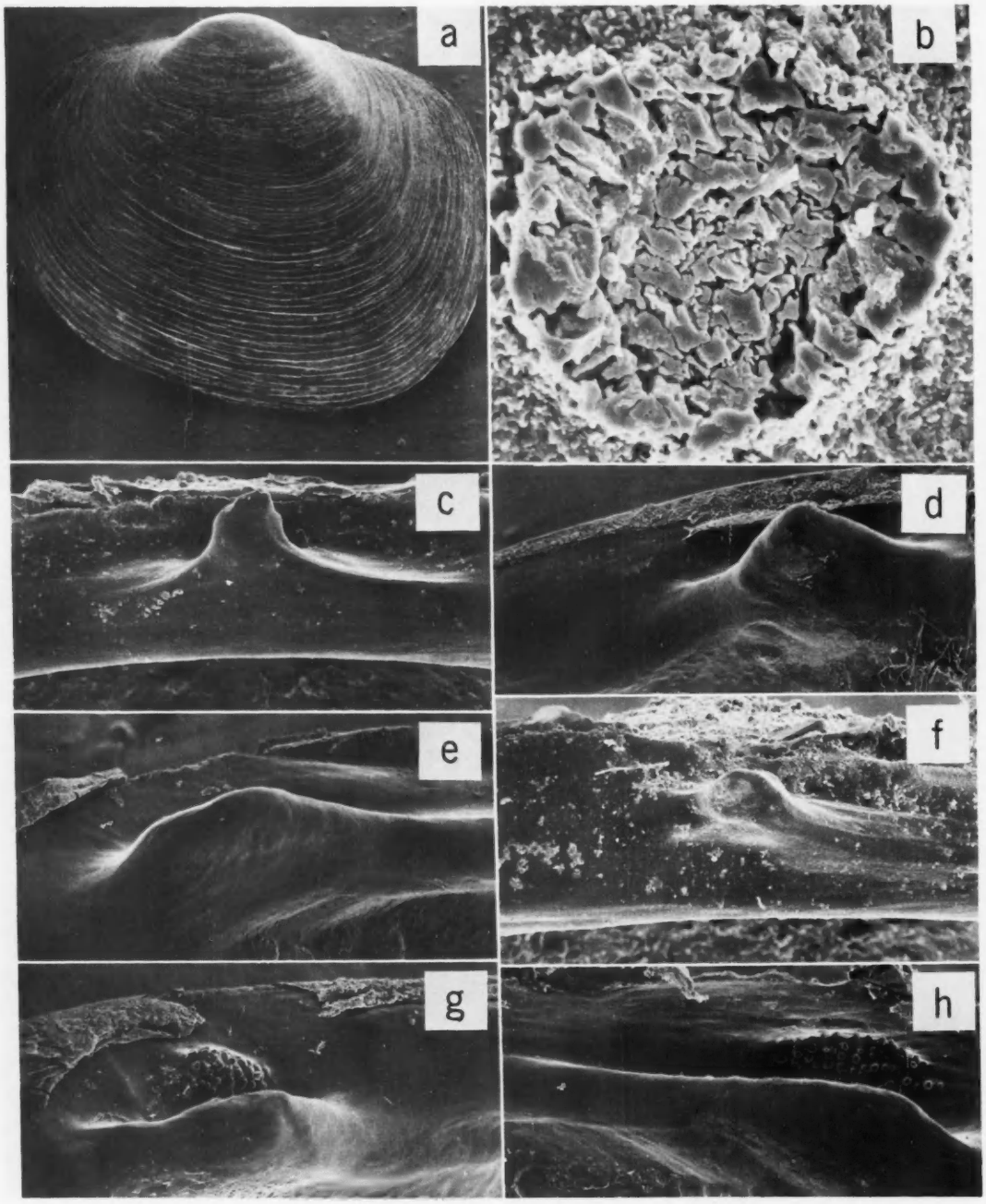

FIG. 1. Shell characteristics of *Eupera cubensis* from the Big Caney River. a, Surface view of left valve showing 34 striae/mm in middle of shell (20×); b, Magnification of one of the adventitious maculations of inner surface of valves (2400×); c, Medial view of C-2 in left valve (260×); d, Medial view of A-II in left valve (52×); e, Medial view of P-II in left valve (52×); f, Medial view of C-3 in right valve 260×); g, Medial view of A-I (nearest) and A-III in right valve (52×). Both cusps bear prominent tubercles on inner faces; h, Medial view of P-I (nearest) and P-III in right valve (52×). Both cusps bear prominent tubercles on inner faces.

TABLE 2. Numbers of three species of bivalves collected in semiquantitative samples from four different habitats in the Big Caney River, Kansas.

Species	Among water willow	Riffle area	Backwater without silt	Backwater with silt
Eupera cubensis	65	1	2	0
Musculium transversum	39	97	43	0
Elliptio complanatus	1	0	0	0

larvae include all developmental stages between the gastrula and the beginning of the formation of the shell; prodissoconch larvae include all developmental stages of shelled larvae while within brood sacs; extramarsupial larvae are those larvae that have escaped from the brood sacs and lie free in the marsupium prior to birth.

Results and discussion — Range extension — The distribution of *E. cubensis* in North America has been thoroughly documented by Heard (1965a). Its occurrence is primarily limited to the southern coastal states of the U.S. from North Carolina to Texas and its presence in Kansas represents a north central range extension. One other additional occurrence has been reported since Heard's (1965a) report; Naqvi and Ferguson (1968) collected several specimens from a ditch near Belzoni, Humphreys Co., Mississippi, and from ponds near State College, Oktibbeha Co., Mississippi.

Habitat characteristics — Table 1 gives some physical and chemical characteritsics of Big Caney River where *E. cubensis* was collected. There are no other data with which to compare or determine water quality criteria of the species. However, Naqvi and Ferguson (1968) demonstrated a significant tolerance of the species to high concentrations of the pesticides, eldrin, and toxaphene.

Table 2 gives the species of bivalves and their relative abundance in the four semiquantitative samples. The data indicate that *E. cubensis* prefers stable substrates associated with root systems of the water willow, *Justicia americana*. This is in general agreement with Walker (1915) who collected the species from rootlets of willow and cypress trees.

Shell characteristics — Using cotypes of *Sphaerium cubense* Prime and the holotype and paratypes of *Sphaerium singleyi* Pilsbry (a junior synonym of *E. cubensis*), Heard (1965a) has given a comprehensive description of the shell of *E. cubensis* but without illustrations. Figures 1a–h are S.E.M. photographs of the most prominent shell characters of *E. cubensis* from the Big Caney River. The photographs support Heard's descriptions of the various types, with one exception: C-3 in shells from the Big Caney River is low, short, and stump-like (Fig. 1f); Heard (1965a) reported C-3 as "high and long, straight and lamellar." Figure 1b is a 2400 × magnification of one of the brown, adventitious maculations on the inner surfaces (only) of the valves and is present on most specimens of *E. cubensis* collected throughout North America (Heard 1965a). Chemical analyses of these crystalline maculations were not made but the brownish color may indicate the presence of iron. The prominent tubercles shown in Fig. 1g and 1h are also characteristic of most species of *Sphaerium* (unpublished S.E.M. photographs). Figure 2 shows that the species has a height to length ratio of 0.77.

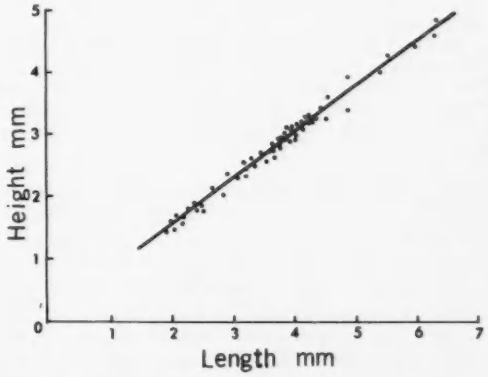

FIG. 2. Length–height relationship of shell of *E. cubensis* from the Big Caney River, Kansas. Line: $Y = 0.77 + 0.02$, $r = 0.97$, $N = 60$.

Brood size — Each embryo is individually encased in a closely adhering tissue which appears to have some connection with the tissues around neighboring embryos. The embryos are usually arranged in one plane and appear to lie free between the inner and outer gill lamellae of the anterior gills. This arrangement contrasts greatly with species of *Pisidium* which have a thick-

TABLE 3. Percent of gravid parents, average size of broods in gravid parents, and average length of shelled larvae in parents of *E. cubensis* in several length classes from Big Caney River, Kansas.

Length-class (*mm*)	No. in class	% gravid	Avg brood size	Avg length of larvae (*mm*)
1.50–1.99	3	0	0	—
2.00–2.49	4	0	0	—
2.50–2.99	6	0	0	—
3.00–3.49	9	16.7	13.0	0.40
3.50–3.99	10	66.7	14.8	0.46
4.00–4.49	14	81.8	19.2	0.53
4.50–4.99	8	100	28.3	0.60
5.00–5.49	2	100	34.0	0.66
5.50–5.99	2	100	48.0	0.68
6.00–6.49	2	50	64.0	0.75

walled sac partitioned into individual chambers, each with a single embryo, and with species of *Musculium* and *Sphaerium* which have one to four thin-walled sacs (per inner demibranch), each containing one or more larvae.

Table 3 gives the percentage of gravid parents (carrying shelled larvae) in several length-classes, the average brood sizes in each length-class of gravid parents, and the average length of larvae in each parental length-class. Most adults were carrying shelled larvae when they reached 4.00 mm in length. Fetal larvae were found in parents less than 3.50 mm long; all larger parents carried prodissoconch larvae. No embryos or extramarsupial larvae were found. All larvae within any one parent appeared to be in the same stage of development.

A strong positive correlation ($r = 0.82$) exists between average brood size and average length (age) of parent, indicating that the generative performance increases with age. Up to 64 larvae were found in parents longer than 6.00 mm. As noted by Heard (1964) in reference to *Eupera platensis* from Argentina, this is greater than the brood sizes in most species of *Pisidium* (1–42; Heard 1965b), *Musculium* (1–35, but 83 reported once for *M. transversum*; Gale 1969; Mackie 1971), or *Sphaerium* (1–21; Avolizi 1971).

Longevity — Up to two annuli were found on some specimens of *E. cubensis* from the Big Caney River. All specimens over 5.50 mm in length had at least one annulus and those greater than 6.25 mm had two annuli. If annuli are yearly marks, as indicated by Heard (1975), these specimens would be in their 3rd yr of life. However, Mackie (1971) and Meier-Brook (1970) cautioned that not all "annuli," particularly in some species of *Musculium* and *Pisidium*, are yearly marks.

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BOOK REVIEWS/COMPTES RENDUS

The Study of Benthic Communities: a Model and a Review. *Robert H. Parker. Elsevier Scientific Publishing Company, Amsterdam, Oxford, New York, 1975. x + 279 p. $32.50.*

R. H. Parker's early investigations were on benthic assemblages in the northern Gulf of Mexico. His interests were in those invertebrates with hard parts that would be preserved in the fossil record. Because his papers were among the few available on the Gulf of Mexico when I began working there a decade ago, I welcomed the opportunity to review his recent work near Woods Hole, Massachusetts. This new book presents the results of intensive bottom sampling within a small heterogeneous harbor in the Elizabeth Islands just off Cape Cod.

The rationale for the book is that an intensive investigation, even though on a small, seemingly unimportant area, can serve as a model for other comparable studies, or presumably those surveys being made for environmental impact statements. From an overwhelming amount of data, Parker has generated numerous maps of the distributions of some of the species and physical variables of the tiny basins. His is one of the few studies that attempts to consider both the distribution of the meiofauna and macrofauna. Factor analysis was utilized to separate different assemblages and the resulting classification is said to differ little from community designations based on subjective comparisons of the areal distributions of species.

Some ecologists gather as much information on a biota and its milieu as possible and then sort out the morass subjectively with distributional maps or with various numerical separations requiring a computer. Another approach is to sample a few parameters very carefully under conditions as controlled as nature will allow and then to look for correlations that are statistically significant among the varying parameters in question. Neither approach is satisfying because correlation is not cause. Parker utilized the first approach: he assembled as much data as possible on everything he could measure. Unfortunately, and perhaps to the detriment of novices who might use his book as a guide, he measured many parameters of little relevance, while overlooking the most important animal groups (polychaete annelids) and the characters of the water and sediment which are undoubtedly very important in controlling animal distribution patterns (oxygen and organic matter). Offering factor analysis as a nostrum for interpreting large quantities of data is a mistake. Most field ecologists, even if they have large computers available to them, should prefer not to have their data taken, as it were, out of their hands. That Parker had little control of this analysis was evidenced when he admitted that "many . . . diagnostic mollusks . . . were inadvertently omitted when the data was prepared for the factor program. . ." (p. 172).

Benthic ecologists today have little trouble defining assemblages in much simpler, objective, and quantitative terms. Of new interest to most of them are such problems as the causes of variations in numbers of species, quantifying energy flow and productivity, resource partitioning, niche width, and competition, and the coupling between pelagic and benthic biological processes. None of these is considered in this book. As a result, while the book represents a record of the occurrences of some of the species living in an elegant, pristine little harbor, it cannot be considered a useful model for studies of marine benthos.

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The European Freshwater Eel. *V. R. P. Sinha and J. W. Jones. Liverpool University Press, Liverpool, England. 1975. xv + 146 p. £6.*

Seven of the eight chapters in this monograph cover in sequence the stages in the life history of the European eel. The eighth chapter provides a general account of commercial fishing methods and the economic value of the species.

The authors have attempted the difficult task of aiming their book at both the biologist and angler with an interest in natural history. The result is a compromise treatment which is not sufficiently exhaustive to be of real value to the eel specialist, and in places is far too detailed and specialized to the layman. The book will probably be of greatest value to a trained biologist wishing to learn about eels but having little prior knowledge of the species.

Many of the data presented in the tables and figures are drawn from papers previously published by the authors. This may have contributed to the rather intensive treatment of selected topics. Admittedly these are important and in some cases controversial aspects of eel biology, but it does lead to rather uneven treatment of the subject as a whole. For example, the chapter dealing with eel distribution is devoted almost entirely to the problems of sex determination. Other subjects covered at length are age determination, the interaction between eels and river-dwelling salmonids, and the Tucker hypothesis concerning the ecophenotypic origin of European eels. The authors go to great lengths to refute Tucker. On the other hand, other aspects of eel biology were either covered briefly or not at all. Both biologist and angler may be interested in topics such as population density, habitat preference, nonspawning movements of eels in freshwater and marine environments, as

well as some of the interesting physiological characteristics of eels. These received but scant attention.

The well-referenced text enriched with numerous line illustrations and tables is both interesting and readable. Although the North American eel is not discussed to any extent, there is sufficient similarity between the biology of the European and American eels, to render the book of interest and value to the North American biologist.

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(R95)

COMING NEXT MONTH / À PARAÎTRE LE MOIS PROCHAIN

Thyasira dunbari n.sp. (Bivalvia: Thyasiridae) from the Canadian arctic archipelago **I. Lubinsky**

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Marine mortality of Puget Sound coho salmon (*Oncorhynchus kisutch*) **S. B. Mathews**

Taxonomy and biology of some Newfoundland marine leeches (Rhynchobdellae: Piscicolidae) **R. A. Khan and M. C. Meyer**

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Temperature selection of juvenile Atlantic salmon (*Salmo salar*) as influenced by various toxic substances **R. H. Peterson**

DDT residues in benthic invertebrates and demersal fish in St. Margaret's Bay, Nova Scotia **B. T. Hargrave and G. A. Phillips**

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Notes

Increased invertebrate drift in an experimental stream caused by electrofishing **P. A. Bisson**

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Reply to D. V. Ellis's comments on a prognosis for Canadian benthic biological oceanography **C. D. Levings**

Chlorinated guaiacols in bleachery wastes: comments on a paper by Leach and Thakore **I. H. Rogers**

Response to the comments of I. H. Rogers **J. M. Leach and A. N. Thakore**

Book Reviews/Comptes rendus

Heavy metals in the aquatic environment. An international conference (P. A. Krenkel [ed.]), **P. V. Hodson**; Statistical calculations—how to solve statistical problems (E. J. Middlebrooks), **J. A. Thomson**

RECENT PUBLICATIONS / RÉCENTES PUBLICATIONS

The number following each title in each series refers to the establishments listed at the end of the section.

Les nombres qui suivent les titres de chacune des séries désignent les établissements suivants à la fin de la section.

Recent Studies

Until 1970, reprints of these articles had been included in an annual volume of "Studies," composed of two parts. The final binding was the 1969 Studies, Part 2, which included No. 1355. These are no longer bound and distributed. We continue, however, to number and list all articles on investigations published in other periodicals, which henceforth may be obtained in reprint form only from the author or originating establishment.

2175. PATERSON, W. D., J. E. STEWART, AND B. M. ZWICKER. 1976. Phagocytosis as a cellular immune response mechanism in the American lobster, *Homarus Americanus*. J. Invert. Pathol. 27: 95–104. (8)

2176. FINDLAY, G. M., G. J. HOWE, AND W. L. LOCKHART. 1974. Impact of Fenitrothion upon Japanese quail (*Coturnix coturnix Japonica*) in a forest ecosystem. Manit. Entomol. 8: 10–14 (4)

2177. LEONHARD, S. L. 1974. Uptake of Fenitrothion by caged crayfish *Orconectes virilis* in Pine Creek, Manitoba, 1973. Manit. Entomol. 8: 16–18. (4)

2178. PERCY, J. A. 1975. Ecological physiology of Arctic marine invertebrates. Temperature and salinity relationships of the amphipod *Onisimus affinis* H. J. Hansen. J. Exp. Mar. Biol. Ecol. 20: 99–117. (5)

2179. DARROW, D. C., AND G. L. FLETCHER. 1975. Effects of drying tritiated testosterone glucuronide and testosterone sulfate on their counting efficiency. Anal. Biochem. 69: 623–626. (7)

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Jusqu'en 1970, ces articles étaient réimprimés, puis reliés dans un volume annuel d'études, comprenant deux parties. Les études de 1969, partie 2, incluant le n° 1355, ont été les dernières à être reliées. Nous n'en faisons désormais plus la reliure ni la distribution. Nous continuons cependant de numéroter les articles et d'en établir des listes d'études sur des recherches mentionnées dans d'autres périodiques. On peut donc se les procurer, sous leur forme réimprimée seulement, de l'auteur ou du service dépositaire.

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336. HALLIDAY, R. G., AND A. T. PINHORN. 1975. Some observations on the theory of fishing. Lunenburg Progress Enterprise. (September 10, 1975, p. 8–9) (9)

337. ROWE, L. W. 1976. Fish habitat protection: guidelines for loggers. DOE FMS Newfoundland Region Information Report Series No. New 1-75-1: 1–16 (9)

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List of Establishments

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Journal of the Fisheries Research Board of Canada

Guide for Authors

A more detailed guide on preparation of manuscripts from theses is available from the Office of the Editor.

Content

We invite submission of manuscripts in the broad field of fisheries management, ocean science, and aquatic environments relevant to Canada.

Articles: Reports of research studies of broad scope that are original contributions to science.

Notes: Differ from papers on the basis of scope or completeness, rather than quality of research. They may be on problems with narrow, readily defined limits; on work that is largely confirmatory; on methodology or research techniques; on advances in knowledge arising as by-products of broader studies; on progress in projects that were discontinued; or on preliminary findings that warrant publication before problems are resolved. They may be organized with as much flexibility as articles except that they have no centered headings and should occupy no more than four printed pages.

Reviews: Detailed articles that are critical appraisals of broad areas of investigation, particularly in fields that have shown rapid development in recent years.

Perspectives: Essays of opinion or hypothesis on fisheries, ocean science, aquatic environments, or related topics that are of concern to the professional and layman. References are desirable; informal style is welcomed.

Letters: Opinion on topics recently under discussion in the *Journal*; preferred maximum length, 500 words. The Editor reserves the right to shorten letters and to make other changes to accord with the style of the *Journal*.

Editorial Practices

The *Style Manual for Biological Journals* (3rd ed. American Institute of Biological Sciences, 3900 Wisconsin Ave. NW, Washington, D.C.) is used as the authority in matters of form. The standards for spelling are: *Webster's Third New International Dictionary* and *le Grand Larousse Encyclopédique*. Titles of periodicals are abbreviated as in the *Biological Abstracts* list. References to literature are made by the name-and-year system. The *Journal* follows the names and spelling recommended in *A List of Common and Scientific Names of Fishes from the United States and Canada* (3rd ed. 1970), Special Publication No. 6 of the American Fisheries Society.

Series titles should be avoided. An *abstract* is required for all manuscripts, and should state concisely, in less than 250 words, what was done, the essentials of the new knowledge, and the main conclusions. Abstracts are published in English and French; those submitted in one language only are translated by the *Journal*.

The Editor normally submits each manuscript to at least two *referees*. Contributors are encouraged to suggest at least four names to be added to the list from which referees may be selected.

Illustrations should be submitted as photographic reproductions no larger than a standard page and must accompany the manuscript. Prints should not be mounted, stapled, or clipped. Symbols, letters, and numerals must be neat, and at least 1.5 mm high when the illustration is reduced to the appropriate size. Drawings should, when possible, be grouped to facilitate comparisons.

Proofs are sent to the author, who is responsible for correcting only errors in typesetting. *Alterations to the content must be avoided.*

Fifty *reprints* are supplied free. Additional reprints may be purchased at the time of publication (an order form is sent out with the galley proof). All orders should be sent to the Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8. Invoices relating to the reprints will be sent out by the Printer. A charge of $40.00 per page is made for articles published. When submitting a manuscript, an author should state that his institution will accept this charge.

Checklist on Manuscripts

Attention to the following questions will expedite appraisal of manuscripts by referees and editors.

Are the findings, interpretations, and conclusions adequately documented and relevant to the purpose of the study?

Are all the tables and figures needed, and organized to facilitate comparisons? Are there inconsistencies between tables or figures and the text, or within the text? Should some of the data be made available separately, in a manuscript report or at a data repository? If you use statistical analysis are the statistics subordinate to the research?

Would any of the text be clearer if condensed? Are summary statements given at the beginning of sections and paragraphs, and are details in sections and paragraphs relevant to their topics? Does the organization of the manuscript follow logically from the statement of purpose in the introduction?

Does the *title* encompass the content of the report?

Does the *abstract* give the essentials of the new knowledge?

Is the *introduction* largely limited to the scope, purpose, and rationale of the study? Is review of the literature limited to defining the problem?

Are details of *materials and methods* limited to what scientists need in understanding the design of the study and in judging adequacy of the data?

Are generalizations on the *results* adequate? Are findings distinguished from inferences from them?

Is *discussion* limited to interpretation and significance of the findings?

Journal de l'office des recherches sur les pêcheries du Canada

Guide des Auteurs

On peut se procurer au bureau du Directeur de la publication un guide plus détaillé pour la préparation de manuscrits à partir de thèses.

Sujets

Nous désirons reçevoir des manuscrits s'insérant dans le vaste domaine de la gestion des pêches, des sciences de la mer et des milieux aquatiques au Canada.

Articles: Comptes rendus d'études d'une portée générale, constituant des contributions inédites à la science.

Notes: Se distinguent des articles par la portée et le degré d'achèvement plutôt que par la qualité des recherches. Elles peuvent traiter de problèmes particuliers et bien définis; de travaux qui sont en grande partie confirmatoires; de méthodologie ou de techniques de recherche; de progrès de la connaissance découlant d'études plus vastes; de développements dans des projets abandonnés; ou de découvertes préliminaires qui méritent d'être publiées avant la solution de problèmes à l'étude. Les notes peuvent être présentées d'une façon aussi souple que les articles, mais elles ne doivent pas porter d'en-têtes centrés ni occuper plus de quatre pages.

Critiques: Articles détaillés constituant une appréciation critique de vastes champs de recherches, particulièrement dans les domaines ayant connu de rapides progrès au cours des dernières années.

Perspectives: Essais d'opinion ou d'hypothèse sur les pêches, les sciences de la mer, les milieux aquatiques, ou sur des sujets connexes qui intéressent professionnels et profanes. Il est préférable de donner des références et d'écrire, si possible, dans un style simple.

Lettres: Opinions sur des sujets exposés dans le *Journal*. Longueur maximale préférable: 500 mots. Le directeur se réserve le droit de raccourcir les lettres et de faire d'autres modifications dans le style du *Journal*.

Dispositions générales

Le *Style Manual for Biological Journals* (3e éd., publié par l'American Institute of Biological Sciences, 3900 avenue Wisconsin N.O., Washington, D.C.) sert de guide quant à la forme de présentation. Le *Webster's Third New International Dictionary* et le *Grand Larousse Encyclopédique* font autorité pour l'orthographe des mots. Les titres de périodiques sont abrégés suivant les *Biological Abstracts*. Les références bibliographiques dans le texte doivent suivre le système nom de l'auteur-année. Pour les noms de poissons et leur orthographe, le *Journal* suit les recommandations contenues dans *A List of Common and Scientific Names of Fishes from the United States and Canada* (Troisième édition, 1970), Publication spéciale No. 6 de l'American Fisheries Society.

Il faut éviter les *articles en série*. Un *résumé* doit accompagner chaque texte et doit exposer brièvement (moins de 250 mots) le travail accompli, les points essentiels des connaissances acquises et les principales conclusions. Les résumés paraissent en anglais et en français, le *Journal* veillant à la traduction dans le cas des présentations unilingues.

Le directeur soumet d'ordinaire chaque texte à l'approbation de deux *arbitres* ou plus. Nous encourageons les collaborateurs à suggérer au moins quatre personnes dont les noms pourraient figurer sur la liste des arbitres.

Les *illustrations* doivent être sous forme de reproductions photographiques ne pas dépasser les dimensions d'une page normale et accompagner le texte. Elles ne doivent pas être montées, coupées ni brochées. Les symboles, lettres ou chiffres doivent se détacher avec précision et avoir au moins 1,5 mm de hauteur lorsque l'illustration est réduite à la grandeur voulue. Les dessins doivent, autant que possible, être groupés pour faciliter l'étude comparative.

L'auteur doit revoir les *épreuves* qu'on lui remet et en corriger seulement les erreurs typographiques. *Il doit éviter de changer le contenu du texte.*

Cinquante *tirés à part* sont fournis gratuitement. Les tirés à part peuvent être achetés au moment de la publication. Un bon de commande à cet effet accompagne les épreuves; il doit être retourné en même temps que celles-ci, non pas au bureau de la rédaction, mais au Printing Department, University of Toronto Press, 5201 Dufferin Street, Downsview, Ont. M3H 5T8, qui se chargera de les facturer. Les frais sont de $40.00 par page pour la publication des articles. Quand un auteur soumet un manuscrit, il doit spécifier que son institution accepte les frais.

Listes de contrôles pour manuscrits

Une attention particulière aux questions suivantes facilitera l'évaluation des manuscrits par les arbitres et les éditeurs.

Les découvertes, interprétations et conclusions sont-elles bien documentées et pertinentes au but de l'étude?

Les tableaux et figures sont-ils tous nécessaires et agencés pour faciliter les comparaisons? Y a-t-il contradiction entre les tableaux ou les figures et le texte, ou dans le texte même? Est-ce que certaines données devraient être présentées séparément, dans un rapport manuscrit ou dans un dépôt de données? Si vous faites une analyse statistique, la statistique cède-t-elle le pas à la biologie?

Le texte y gagnerait-il en clarté s'il était plus condensé, en tout ou en partie? Contient-il des exposés sommaires au début de chaque section ou paragraphe, et les détails de ces sections et paragraphs son-ils pertinents au sujet traité? La marche du manuscrit est-elle conforme à la logique énoncée dans l'introduction?

Le *titre* est-il concis, tout en étant représentatif du contenu du rapport?

Le *résumé* donne-t-il l'essentiel des connaissances nouvelles?

L'*introduction* se limite-t-elle à une esquisse de la portée, du but et des raisons de l'étude? La revue de la littérature se limite-t-elle à la définition du problème?

La section *matériel et méthode* contient-elle le minimum de détails qui permettront aux autres scientifiques de saisir les grandes lignes de l'étude et de juger de la valeur des données?

Les généralisations sur les *résultats* sont-elles adéquates? Permettent-elles de distinguer entre constatations et déductions?

La *discussion* est-elle limitée à l'interprétation et à l'évaluation des découvertes?

Journal of the Fisheries Research Board of Canada

Guide for Typists Preparing Copy

Read "Guide for Authors" in the current volume of the *Journal*. When in doubt about how to type or arrange details, follow *Journal* practice.

Type the manuscript on white bond paper, not flimsy, preferably size 21.5 × 28 cm (8.5 × 11 inches). If possible, use paper with the lines numbered in the margin. Leave all margins at least 2.5 cm wide.

Double-space all parts of the manuscript, including tables, captions for illustrations, footnotes, and the reference list. Underline only material that is to be printed in italics. Indent the first line of each paragraph in the text and of each footnote.

In titles and headings, capitalize the first letter of each word. For small capitals, use small letters.

Indicate all text footnotes by superscript arabic numerals. Number them consecutively throughout the manuscript, starting with those on the title page. Place each footnote immediately below the reference to it, separating it from the text by horizontal lines.

On the first page type only the title, the authors' names and affiliations, related footnotes, and the running head (see Appendix A). Type the abstract on a separate page (see Appendix B). Number all pages, beginning with the title page and including those for tables and captions for illustrations.

Have the author check the finished manuscript, and send the ribbon copy and two other clear copies to the Office of the Editor.

Tables: Examine the current volume of the *Journal* to see how tables are set up (see Appendix C).
Note especially the following concerning *numbered tables:*

Type each on a separate page, using paper without the lines numbered.

Number them with arabic numerals.

Use horizontal lines above and below the headings and below the columns, and seldom elsewhere. Never use vertical lines; leave extra spaces instead.

Indicate table footnotes by superscript small letters and type them below the table.

Place the tables after the list of references.

Where each table is first referred to, type in the margin "Table — near here."

Note that *text tables* are not numbered, are typed with the text, and seldom need horizontal lines (see Appendix C).

Illustrations: Send a photographic reproduction (no larger than 21.5 × 28 cm) of each illustration with the manuscript. Type the author's name and figure number on a strip of paper and fasten it to the back of the print. Do not write or type on the print itself. Also, type the captions in succession on a separate page, headed "Captions for illustrations." Put this page at the end of the manuscript.

Where each figure is first referred to, type in the margin "Fig. — near here."

Mathematical Expressions, Equations, and Formulas: Leave three spaces above and below lines that have much material in superscripts, and above and below equations and formulas. In the various expressions, place each component in its correct position (see Appendix D).

Show all symbols clearly. In the margin, spell out Greek letters the first time they occur, and distinguish between the small letter *l* and the numeral *one*, and between the capital letter *O* and the numeral *zero*. Make other explanatory notes similarly.

References: Check the text to see that all references in the list are referred to. Type the reference list, double-spaced, in the style used in the *Journal* (see Appendix E). Names of journals are abbreviated as in the *Biological Abstracts* list; if an abbreviation is in doubt, type the name in full.

Spellings: About 100 words common in fisheries journals are listed in Appendix F.

Appendices: Appendices A to F are available on request from the Office of the Editor.

Journal de l'office des recherches sur les pêcheries du Canada

Guide pour les secrétaires d'auteurs

Lisez le "Guide des Auteurs" reproduit dans l'édition courante du *Journal*. Si vous avez des doutes sur la façon de dactylographier le texte ou d'en agencer les détails, suivez la pratique du *Journal*.

Dactylographiez le manuscrit sur papier blanc de bonne qualité, et non sur papier pelure, mesurant de préférence 21,5 × 28 cm (8,5 × 11 pouces), laissant toujours une marge d'au moins 2,5 cm. Si possible, employez un papier avec lignes numérotées en marge.

Tout le manuscrit, y compris tableaux, légendes de figures, renvois et références bibliographiques, devra être dactylographié à double interligne. Ne soulignez que les mots qui devront être imprimés en italique. Mettez en retrait la première ligne de chaque paragraphe du texte et de chaque renvoi.

Dans les titres et les en-têtes, n'employez la majuscule que pour le premier mot et les noms propres. Pour les petites majuscules, employez les miniscules du dactylographe.

Indiquez tous les renvois du texte par des chiffres arabes suscrits. Numérotez les renvois consécutivement par tout le texte, à commencer par ceux de la page titre. Placez chaque renvoi directement sous sa référence, le séparant du texte par des lignes horizontales.

La première page ne doit contenir que le titre de la publication, le nom et l'affiliation des auteurs, les renvois appropriés et le titre courant (voir Appendice A). Dactylographiez le résumé sur une page séparée (voir Appendice B). Numérotez chaque page, à commencer par la page titre, y compris celles qui contiennent les tableaux et la légende des figures.

Voyez à ce que l'auteur vérifie le manuscrit final, et soumettez la première copie ainsi que deux copies lisibles au bureau du Directeur de la publication.

Tableaux. Consultez une copie du *Journal* pour la composition des tableaux (voir Appendice C).

Portez une attention particulière à ce qui suit au sujet des *tableaux numérotés*.

Dactylographiez chaque tableau sur feuille séparée, vous servant de papier sans lignes numérotées.

Numérotez les tableaux en chiffres arabes.

Tracez des lignes horizontales au-dessus et au-dessous des en-têtes et au-dessous des colonnes, rarement ailleurs; ne tracez jamais de lignes verticales; laissez plutôt des espaces supplémentaires.

Indiquez les renvois dans les tableaux par les minuscules suscrites et placez les renvois au bas du tableau.

Placez les tableaux à la suite des références bibliographiques.

A l'endroit où le tableau est mentionné pour la première fois, indiquez dans la marge "Tableau — près d'ici."

Remarquez que les *tableaux dans le texte* ne sont pas numérotés, sont dactylographiés avec le texte et ne requièrent que rarement des lignes horizontales (voir Appendice C).

Figures: Envoyez avec le manuscrit un reproduction photographique (21,5 × 28 cm ou moins) pour chaque illustration. Dactylographiez le nom de l'auteur et le numéro de la figure sur une lisière de papier que vous collerez au dos. N'écrivez pas à la main ou à la machine sur la photographie même. En plus, dactylographiez les légendes, dans l'ordre, sur feuille séparée, intitulée "Légendes des figures." Intercalez cette feuille à la suite du texte.

A l'endroit où chaque figure est mentionnée pour la première fois, inscrivez en marge "Fig. — près d'ici."

Equations, formules et expressions mathématiques: Laissez trois espaces au-dessus et au-dessous des lignes renfermant des chiffres ou des lettres suscrits et souscrits, ou encore au-dessus et au-dessous d'équations et de formules. Placez chaque composante des différentes expressions dans la position qui lui est propre (voir Appendice D).

Indiquez clairement tous les symboles. Epelez en marge les lettres grecques, la première fois qu'elles apparaissent. Faites une distinction entre la lettre *l* et le chiffre *un*, et entre la majuscule *O* et le chiffre *zéro*. Insérez de la même façon toute autre note explicative.

Références: Vérifiez le texte afin de vous assurer que toutes les références apparaissant dans la liste bibliographique sont bien mentionnées dans le texte. Dactylographiez à double interligne dans le style en usage dans le *Journal* (voir Appendice E). Les noms de revues sont abrégés suivants les *Biological Abstracts*; en cas de doute, écrivez le nom au long.

Orthographe: Une liste d'environ 100 mots communément employés dans les périodiques sur les pêches est donnée en Appendice F.

Appendices: On peut se procurer une copie des Appendices A à F sur demande au bureau du Directeur de la publication.

ADVANCE ANNOUNCEMENT

FISHERIES SOCIETY OF THE BRITISH ISLES

A Symposium will be held at the University of Stirling, from July 4–8, 1977 on: *Rhythmic Activity of Fish*

Hormonal Controls
Behavioral Rhythms
Community Relationships
Methods and Instruments

Contributors will include:

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W. R. A. Muntz, University of Stirling, Scotland
I. G. Priede, University of Aberdeen, Scotland
H. O. Schwassmann, University of Florida, USA
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T. H. Simpson, DAFS, Marine Laboratory, Aberdeen, Scotland
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Further details of the program, bookings, etc., will be obtainable in October 1976 from the symposium organizer:

J. E. Thorpe
Freshwater Fisheries Laboratory
Pitlochry
Perthshire, PH16 5LB
Scotland

PREAVIS

FISHERIES SOCIETY OF THE BRITISH ISLES

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Contrôles hormonaux
Ryhtmes de comportement
Relations entre les communautés
Méthodes et instruments

Parmi les contributeurs, il y aura:

H. Braithwaite, Université de Birmingham, Angleterre
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D. J. Staples, CSIRO, Karumba, Australie
T. Storeton-West, MAAF, Laboratoire maritime, Lowestoft, Angleterre

On pourra se procurer en octobre 1976 plus de détails sur le programme, les réservations, etc., en s'adressant à l'organisateur du colloque:

J. E. Thorpe
Freshwater Fisheries Laboratory
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Perthshire, PH16 5LB
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Bulletin of the Fisheries Research Board of Canada

Bulletin 188F Ottawa 1975

L'Aquiculture au Canada

Présent et avenir

H.R.MacCrimmon
J.E.Stewart
J.R.Brett

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Announcement

When *Fishes of the Atlantic Coast of Canada*, Fisheries Research Board Bulletin 155, by A. H. Leim and W. B. Scott, was published in 1966, an early revision was planned. That revision was postponed, however, in favor of *Freshwater Fishes of Canada* (FRB Bulletin 184).

The revision of Bulletin 155 is now under way. The cooperation and support of everyone interested in Atlantic marine fishes is earnestly solicited. Records of unusual occurrences, behavior, or observations on other aspects of the biology, game or commercial importance of the fishes in the region would be welcomed. Comments or criticisms of the original volume itself would also be useful.

Comments may be addressed directly to Dr. W. B. Scott, Huntsman Marine Laboratory, Brandy Cove, St. Andrews, New Brunswick, or to the Department of the Environment, Fisheries and Marine Service, Office of the Editor, Journal of the Fisheries Research Board of Canada, 116 Lisgar St., Ottawa K1A 0H3.

Avis

Lors de la publication, en 1966, du bulletin n° 155 de l'Office des recherches sur les pêcheries intitulé *Poissons de la côte atlantique du Canada*, par A. H. Leim et W. B. Scott, on avait projeté de le réviser sous peu. Cette révision a cependant été retardée en faveur du bulletin 184 de l'ORP, intitulé *Poissons d'eau douce du Canada*.

La révision du bulletin 155 est en cours. La collaboration et l'appui de tous ceux qui s'intéressent aux espèces marines de l'Atlantique seraient grandement appréciés. Tout compte rendu de faits inhabituels, de comportements ou d'observations d'autres aspects importants des poissons de la région sur les plans biologique, sportif ou commercial serait bienvenu. Les commentaires ou critiques sur le volume original pourraient également être utiles.

Les commentaires peuvent être adressés directement à M. W. B. Scott, Laboratoire Huntsman de sciences marines, anse Brandy, St. Andrews (Nouveau-Brunswick) ou au Ministère de l'Environnement, Service des pêches et des sciences de la mer, Bureau du rédacteur du Journal de l'Office des recherches sur les pêcheries, 116, rue Lisgar, Ottawa K1A 0H3.

Journal of the Fisheries Research Board of Canada

Journal de l'Office des recherches sur les pêcheries du Canada

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Volume 33, No. 7, July 1976

Volume 33, n° 7, juillet 1976

Review of the rate of growth and mortality of Pacific salmon in salt water, and noncatch mortality caused by fishing **W. E. Ricker** 1483–1524

Production of wild, domestic, and interstrain hybrids of brook trout (*Salvelinus fontinalis*) in natural ponds **W. A. Flick and D. A. Webster** 1525–1539

Effect of temperature and salinity on extension of siphons by *Mercenaria mercenaria* **W. Van Winkle, S. Y. Feng, and H. H. Haskin** 1540–1546

Azygokeras columbiae, a new genus and species of marine epibenthic copepod (Calanoida: Aetideidae) from British Columbia **P. A. Koeller and J. L. Littlepage** 1547–1552

Autotrophic production in Carnation Creek, a coastal rainforest stream on Vancouver Island, British Columbia **J. G. Stockner and K. R. S. Shortreed** 1553–1563

A natural epizootic of infectious hematopoietic necrosis in fry of sockeye salmon (*Oncorhynchus nerka*) at Chilko Lake, British Columbia **I. V. Williams and D. F. Amend** 1564–1567

Effects of mercury and copper on the olfactory response in rainbow trout, *Salmo gairdneri* **T. J. Hara, Y. M. C. Law, and S. Macdonald** 1568–1573

Distribution, age and growth, and sexual maturity of witch flounder (*Glyptocephalus cynoglossus*) **W. R. Bowering** 1574–1584

Influence of bovine growth hormone and L-thyroxine on growth, muscle composition, and histological structure of the gonads, thyroid, pancreas, and pituitary of coho salmon (*Oncorhynchus kisutch*) **D. A. Higgs, E. M. Donaldson, H. M. Dye, and J. R. McBride** 1585–1603

Effects of crude oil on American lobster (*Homarus americanus*) larvae in the laboratory **P. G. Wells and J. B. Sprague** 1604–1614

Utilization of artificial shelters by the American lobster (*Homarus americanus*) **D. J. Sheehy** 1615–1622

Evidence for the presence of molt-inhibiting hormone in the sinus gland of the lobster *Homarus americanus* **E. F. Couch, C. S. Daily, and W. B. Smith** 1623–1627

Notes

An inexpensive tag for short-term visual tracking studies **B. M. Leaman** 1628–1629

Analyses of gastric emptying in bluegill (*Lepomis macrochirus*) **F. M. El-Shamy** 1630–1633

Variations in fillet lipid content and some percent lipid-iodine value relationships for large winter Atlantic herring (*Clupea harengus harengus*) from southeastern Newfoundland **R. G. Ackman and C. A. Eaton** 1634–1638

Life history notes for a population of slimy sculpin (*Cottus cognatus*) in an Alaskan arctic stream **P. C. Craig and J. Wells** 1639–1642

Occurrence of the woodborer, *Limnoria lignorum* (Rathke) at Amchitka Island, Alaska **B. R. Richards and C. I. Belmore** 1642–1644

Growth per molt and limb regeneration in the spider crab, *Chionoecetes opilio* **R. J. Miller and J. Watson** 1644–1649

An index of fish movement with statistical techniques for its interpretation **E. P. Bergersen and T. J. Keefe** 1649–1652

Biological notes on *Eupera cubensis* (Bivalvia: Sphaeriidae) from Kansas **G. L. Mackie and D. G. Huggins** 1652–1656

Book Reviews/Comptes rendus

The study of benthic communities: a model and a review (R. H. Parker), **G. T. Rowe**; The European freshwater eel (V. R. P. Sinha and J. W. Jones), **J. G. Eales** 1657–1658

Coming next month/À paraître le mois prochain 1659

List of recent publications/Liste de récentes publications 1660–1664

Guide for authors and typists/Guide des auteurs et Guide pour les secrétaires d'auteurs *i–v*

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